

Impact of Human Recreational Activities on Forest Birds

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SUMMARY

Outdoor recreation has increased in popularity through development in infrastructure and transportation, as well as an enormous diversity and specialisation of clothing and gear. Although no harm is intended by recreationists and in some cases actually the opposite (i.e. ecotourism) is the goal, recreation has negative consequences for wild species. Thus, a great amount of research is being done by concerned researchers to try to understand the magnitude of the negative impact of human disturbance.

However, these studies usually have two main caveats. First, they fail in disentangling direct effects of human presence from effects of habitat modifications (e.g. trails or roads) linked to outdoor recreation. Secondly, many studies are done in areas where human disturbances have been occurring already for a long period of time, which may lead to wildlife already being “adapted” (either behaviourally or through pre-selection of individuals inhabiting those areas) to these disturbances, and thus obscure the complete magnitude of the human disturbance impact.

In this thesis we aimed to deal with these two problems through a combination of well-thought comparative and experimental studies. We focused on forested habitats, because forests are a widespread habitat worldwide and frequently used for recreational activities.

In the **first chapter** we were interested in separating the direct human effect from the potential indirect effect of habitat change through recreational trails. Therefore we selected four different forests with a similar network of trails, strongly differing in their human frequentation. Two of them were heavily frequented by humans for recreation whereas the other two were rarely used for human recreation. We used a paired point count design to census the breeding birds in these four forests, with a point count close to a trail and a paired adjacent count further away from the same trail to test how the effect of

the trail varied across forests depending on the amount of visitors. We also investigated how the effect of the trails/human disturbance is modulated by the characteristics of the species. Birds in heavily frequented forests avoided trail proximity; there was a difference in bird abundance of 13% between the close and the far point count, whereas there was no difference between paired point counts in unfrequented forests. Similarly species richness dropped by 12% between the close and its paired far point count in heavily frequented forests, whereas there was no difference in unfrequented forests. Looking at the nesting guilds in unfrequented forests revealed a tendency for ground nesters to prefer trail proximity, whereas there was no trail effect on cavity and open-cup nesters. In heavily frequented forests, cavity nesters as well as open-cup nesters avoided trail proximity, whereas ground nesters showed no effect. These findings imply, besides some species-specific differences, that the direct impact of humans using the trails is the stronger driver for bird composition compared to the indirect impact of habitat changes through trail construction.

In **chapter two** we examined whether birds in highly frequented forests are truly responding less to humans than in forests which are hardly frequented by humans. For that we focused on the antipredatory response, more specifically on flight initiation distance (FID), which is the distance at which a bird flushes from an approaching human. We measured FID in both heavily and rarely frequented forests during the same time of the year for nine forest-bird species. FIDs of most species were larger in the unfrequented forest compared to FID in the frequented forests. This could be explained by birds learning that humans are not a threat and tolerating human presence (habituation) or by human presence acting as a selection factor on personality, with the result that only the most tolerant individuals stay, whereas the shy individuals leave the area.

In the **third chapter** we focused on the least frequented forest to experimentally investigate how the presence of humans during the early spring actually affects territory

selection of birds. Therefore, we split forest plots into two halves (split-plots). In one half we walked through the forest without trails, mimicking people hiking, during March to mid-April, and compared the later breeding bird communities between these split-plots and the un-frequented ones. Forest-bird abundance as well as species richness were both reduced by 15% in human frequented plots compared to control plots. This result shows that human presence directly affects a bird's decision where to settle, independently of vegetation characteristics.

Finally, in **chapter four** we studied the potential trans-generational effects of the experimental recreation (preceding chapter) on the individuals that settled, through examining maternal antibody deposition into the eggs of two breeding tit species (Great tits *Parus major* and blue tits *Cyanistes caeruleus*). We measured the amount of total antibodies in six days old tit nestlings (at that age they still rely mainly on maternal antibodies) and compared nestlings hatched in experimentally disturbed split-plots with hatchlings from unfrequented controls. We found a negative effect of the experimental human presence on maternal antibody deposition for great tits, but not for blue tits. Great tits breeding in disturbed split-plots deposited fewer maternal antibodies into their eggs compared to great tits breeding in control split-plots. This disturbance impact was dependent on the vegetation density; with a higher shrub cover lowering the disturbance impact on maternal antibody deposition. For great tits, the amount of maternal antibodies had a positive effect on hatching success and chick weight, both independent of human presence. For blue tits, these results could not be confirmed, instead we found that the presence of great tits was the stronger driver than the experimental disturbance. This study showed, that even low intensities of human recreation (as ours) can stress breeding birds so much, that an immunosuppressive reaction was measurable via maternal antibody deposition, and a trans-generational effect could be confirmed.

Human presence in forests drives breeding bird densities and species richness and, depending on the intensity and duration of recreational activities, could have long term consequences for the avifauna. As these human impacts on wildlife will certainly increase in the future, effective conservation measures are needed. Such measures necessarily include protected wildlife areas with reduced or prohibited access for humans. Outdoor recreational activities should be well guided, mainly through a clever trail-network, bypassing rare species' home ranges and/or habitats, for their conservation. Through such smart conservation measures most outdoor recreationists will not be limited in their activities, but it would allow both, wildlife and recreationists to persist side by side.

Author's contribution:

Yves Bötsch's contributions to each chapter include:

- Authored general introduction
- Chapter 1: Study design and planning, data collection of first year, supervision of Bachelor student Daniel Scherl (data collection during second year), data analyses and publication (main author)
- Chapter 2: Study design, part of data collection during the first year, supervision of Selina Gugelmann (data collection during second year, Semester work), data analyses and publication (main author)
- Chapter 3: Study design and planning, data collection, analyses and publication (main author)
- Chapter 4: Study design, blood sample collection, laboratory work, data analyses and publication (main author)
- Authored general discussion

ZUSAMMENFASSUNG

Freizeitaktivitäten in der Natur haben in den letzten Jahrzehnten an Popularität gewonnen. Durch moderne Infrastrukturen sowie spezialisierte Ausrüstung wurden viele Aktivitäten für die breite Öffentlichkeit zugänglich gemacht. Obwohl die meisten Erholungssuchenden der Natur nicht schaden wollen, ja sich sogar an ihr erfreuen, können ihre Aktivitäten negative Folgen für Wildtiere haben. Damit man den Einfluss der Freizeitaktivitäten messen und verstehen kann, wird weltweit viel Forschung betrieben. In diesen Studien gibt es zwei problematische Punkte: Erstens können die meisten Studien direkte Effekte durch die Präsenz von Menschen nicht von Habitatveränderungseffekten durch die Infrastruktur (z.B. Wege) trennen. Zweitens werden viele Studien in Gebieten durchgeführt, in welchen schon seit langer Zeit Freizeitaktivitäten stattfinden und die lokale Tierwelt sich bereits an diese Aktivitäten gewöhnt haben könnte (angepasstes Verhalten oder Selektion von störungstoleranten Individuen), was dazu führen kann, dass die Grössenordnung des Einflusses der Freizeitaktivitäten unterschätzt wird.

Das Ziel dieser Arbeit war, diese beiden Schwierigkeiten mit gut geplanten, vergleichenden sowie experimentellen Studien zu umgehen. Wälder sind ein weit verbreitetes Habitat in Europa und ein beliebter Ort für verschiedenste Freizeitaktivitäten, weshalb wir unseren Forschungsschwerpunkt auf diesen Habitat-typ legten.

Im **ersten Kapitel** wollten wir den direkten Effekt der menschlichen Präsenz mit dem indirekten Effekt der Habitatveränderung durch Wege vergleichen. Dazu wählten wir vier verschiedene Wälder mit einem ähnlichen Wanderwegenetz, aber einer stark unterschiedlichen Frequentierung aus. Zwei davon werden selten begangen, während die anderen beiden Wälder in Stadtnähe sehr oft für Freizeitaktivitäten benutzt werden. Wir führten in diesen Wäldern paarweise Punkt-Stopp-Zählungen durch. Eine Zählung fand nah und eine weiter entfernt von einem Wanderweg statt, um zu testen, wie sich

Habitatveränderungen durch Wege und menschliche Präsenz auf die Vogelwelt auswirken. Des Weiteren untersuchten wir, wie sich die Effekte Weg und Begehungsintensität auf unterschiedliche Artgruppen auswirkten. Die Vögel mieden die wegnahen Punkte in Wäldern, welche oft begangen werden (Abundanz um 13% reduziert im Gegensatz zu den weiter entfernten Flächen), wogegen in selten begangenen Wäldern kein Unterschied zwischen wegnahen und wegfernen Punkten festgestellt wurde. Einen ähnlichen negativen Effekt (-12%) zeigte sich auch für die Artenzahl in oft begangenen Wäldern. In wenig begangenen Wäldern konnten wir eine leichte Präferenz von Bodenbrütern für wegnahen Punkte feststellen; hingegen zeigten Höhlenbrüter sowie Offenbrüter keinen Unterschied zwischen wegnahen und wegfernen Punkten (Abundanz und Artenzahl). In den oft begangenen Wäldern wurden die wegnahen Punkte vor allem von Höhlenbrütern und Offenbrütern gemieden, wo hingegen Bodenbrüter keinen Effekt zeigten. Diese Resultate zeigen, dass neben gewissen Artgruppen spezifischen Effekten, die menschliche Präsenz der stärkere Treiber gegenüber weginduzierten Habitatveränderungen darstellt.

Im **zweiten Kapitel** testeten wir, ob Vögel in häufig begangenen Wäldern tatsächlich weniger stark auf Menschen reagieren im Vergleich zu Vögeln aus selten begangenen Wäldern und somit den Effekt der Störung verwaschen. Wir haben dazu unser Augenmerk auf die Fluchtdistanz gelegt, d.h. die Distanz, bei welcher ein Vogel von einem sich annähernden Menschen flüchtet. Wir haben Fluchtdistanzen von neun Vogelarten zur gleichen Jahreszeit in häufig begangenen und selten begangenen Wäldern gemessen. Die Fluchtdistanzen der meisten Vogelarten waren im selten begangenen Wald grösser als in den häufig begangenen Wäldern. Möglicherweise entstehen die Fluchtdistanz-Differenzen zwischen häufig begangenen und wenig begangenen Wäldern durch eine erlernte Toleranz gegenüber Menschen (Habituation) oder durch eine Selektion

von Individuen, die die Anwesenheit von Menschen tolerieren, und eine Abwanderung von menschen-intoleranten Individuen bewirkt (Individualität).

Im **dritten Kapitel** untersuchten wir mit einem experimentellen Ansatz den direkten Einfluss von Wanderern auf das Ansiedlungsverhalten von Waldvögeln. Dazu wanderten wir 2-3 Mal täglich während der Ansiedlungsphase der Brutvögel (März bis Mitte April) durch Waldflächen ohne Wegenetz und verglichen danach die Brutvogel Gemeinschaften zwischen diesen begangenen Flächen und unbegangenen Kontrollflächen. Die Abundanz der Waldvögel sowie ihr Artenreichtum waren auf den begangenen Flächen beide um 15% geringer als auf den nicht begangenen Kontrollflächen. Dies zeigt, dass menschliche Präsenz unabhängig von der Vegetationsstruktur das Ansiedlungsverhalten von Waldvögeln direkt beeinflusst.

Dies leitet direkt über zu **Kapitel vier** wo wir den möglichen Effekt der experimentellen Störungen (siehe vorangehendes Kapitel) auf die Übertragung von maternalen Antikörpern in die Eier untersuchten. Dazu haben wir die Antikörpertiter von sechs Tage alten Blau- und Kohlmeisen-Nestlingen gemessen, da ihre Antikörper in diesem Alter noch hauptsächlich von der Mutter stammen. Wir verglichen die Titer der in den von uns begangenen Flächen geschlüpften Küken mit denen von Küken aus den unbegangenen Kontrollflächen. Kohlmeisen-Nestlinge, welche in experimentell gestörten Flächen schlüpften, hatten tiefere maternale Antikörpertiter als Jungmeisen, welche in ungestörten Flächen schlüpften. Dieser Effekt war aber abhängig von der Vegetationsdichte; dichtere Vegetation reduzierte den Störungseinfluss auf die maternalen Antikörpertiter. Generell stellten wir fest, dass der Antikörpertiter bei Kohlmeisen mit der Schlupfrate sowie mit dem Gewicht der Jungmeisen positiv korrelierte. Bei den Blaumeisen konnten wir, ausser der Korrelation zwischen den Antikörpertitern und dem Körpergewicht der Jungmeisen, keinen der gefunden Effekte nachweisen. Bei den Blaumeisen schien es, dass die Anwesenheit von Kohlmeisen der stärkere beeinflussende

Faktor darstellte als unsere Störung. Die geringe Intensität an experimenteller menschlicher Aktivität störte die Kohlmeisen während der Eiablage offenbar so stark, dass deren erhöhter Stresshormonspiegel (Corticosteron) seine immunsuppressive Funktion ausüben konnte, und wir diese via maternale Antikörpertiter in den Nestlingen feststellen und somit einen inter-generationen Effekt aufzeigen konnten.

Die Anwesenheit von Menschen in Wäldern beeinflusst also die Abundanz der Brutvögel sowie deren Artenzahl und kann in Abhängigkeit von der Intensität und Dauer von Freizeitaktivitäten mögliche Langzeitfolgen haben. Die Ausweisung von Schutzgebieten mit eingeschränktem oder unterbundenem Zugang für Besucher scheint daher eine angebrachte Naturschutzmassnahme zu sein. Damit seltene Arten oder Lebensraumtypen erhalten werden können, sollten Freizeitaktivitäten in der Natur mit durchdachten Wegführungen gelenkt werden. Durch solche Massnahmen können die Ansprüche von Wildtieren und von Erholungssuchenden gleichermassen erfüllt und ein einvernehmliches Miteinander garantiert werden.

GENERAL INTRODUCTION

Pressure on nature

Human impacts on habitats and wildlife increase unrestrictedly, as the world population is growing steadily (Gerland *et al.* 2014). Natural habitats not only are affected by the mere living space needed for the human population along with the need for food-producing cultivated area. Also human recreation activities commonly occur in nature. New recreational activities (e.g. stand-up paddling) with its infrastructure are developed as well as vast amounts of specialized clothing and gear. Therefore outdoor recreation entails a large economic sector, still booming nowadays (Balmford *et al.* 2009). The vast majority of outdoor recreationists are not interested in directly enjoying nature (e.g. fauna and flora observations), but in outdoor sport-activities, from the most popular hiking/jogging to more specialized activities like paragliding, downhill cycling or rock climbing. More and more previously pristine and unfrequented habitats, from steep rock faces to white water, become used by humans.

Being outdoors has been shown to positively affect human health and well-being (Martinez-Juarez *et al.* 2015). Even the willingness to spend money for conservation is positively affected by former experience with nature (Zaradic, Pergams & Kareiva 2009). Therefore “allowing” humans to get in contact with nature has positive consequences for both humans and nature conservation. Nevertheless, human outdoor activities affect wildlife and direct wildlife observations and photography, known as ecotourism and “non-consumptive” activity (Wilkes 1977; Goodwin 1996), also impact wildlife (Müllner, Linsenmair & Wikelski 2004). We also cannot deny research(er) related effects on wildlife/natural habitats (Götmark 1992). In the following paragraphs I will point out the effects of outdoor recreation on wildlife as well as demonstrate activity and habitat dependent modulators of wildlife reactions.

Effects of outdoor activities

Direct effects

Outdoor-activities can impact wildlife immediately, as humans are often perceived by animals as predators (Frid & Dill 2002); therefore animals flush or hide. Besides consumptive activities like fishing and hunting, also collisions with cars can directly be lethal (Clevenger, Chruszcz & Gunson 2003).

Frightened animals can show a behavioural reaction and/or may trigger a physiological one, non-detectable from the outside (Müller *et al.* 2006; Thiel *et al.* 2008; Almasi *et al.* 2015; Arlettaz *et al.* 2015). These direct impacts can have drastic effects for animals, as they lose energy through escaping from the threat, or via increased physiological demands, as for example an activation of the HPA-axis (Hypothalamic Pituitary Adrenal) and/or the cardiac system (Romero, Soma & Wingfield 1998; Sapolsky, Romero & Munck 2000; Nephew, Kahn & Romero 2003; Romero 2004). Such physiological reactions can negatively affect the animal's survival, as for example chronically elevated levels of stress hormones (corticosterone or cortisol) negatively affect an individual's immune system (Saino *et al.* 2003; French *et al.* 2010).

Human presence can also alter the animal's spatial and/or temporal space use (Ciucci *et al.* 1997; Olson, Squibb & Gilbert 1998) or even cause the desertion (local extinction) of a given area (Boyle & Samson 1985; Garber & Burger 1995). Moreover the individual's reproductive output and later also the offspring's survival can be directly affected through human presence (Safina & Burger 1983, but see also **Seasonality and habitat** below).

Indirect effects

Many outdoor activities rely on some kind of infrastructure (e.g. ski lift), with trails and roads being the most common ones (from now on referred to as trails). The

construction of trails entails a dramatic change in vegetation, soil surface and altered water balance (Benninger-Truax, Vankat & Schaefer 1992; Trombulak & Frissell 2000). Besides the direct change (reduction) in habitat, an additional important factor joins in, namely fragmentation. Habitats not only get smaller through trail construction but become also more and more fragmented, separating wildlife populations and reducing gene-flow (Saunders, Hobbs & Margules 1991; Reed, Johnson-Barnard & Baker 1996; Forman & Alexander 1998; Trzcinski, Fahrig & Merriam 1999; Bregman, Sekercioglu & Tobias 2014). Additionally trails can facilitate access of predators, which consequently increases predation risk and lowers habitat suitability for the local species/individuals (Miller, Knight & Miller 1998).

Therefore outdoor activities often affect wildlife indirectly, e.g. via changing the habitat. Depending on disturbance intensity, indirect effects on wildlife become detectable only after a certain period of time (Steven, Pickering & Castley 2011; Monz, Pickering & Hadwen 2013), but are then long-lasting, compared to some direct/short-time effects.

Factors modulating the effects of human disturbance

The severity of human recreation impacts can be modulated through several factors, which are described in the three following paragraphs.

Type of leisure activity

Not all types of recreational activities have the same impact on wildlife. The predictability of a given activity plays an important role; activities with a predictable direction are perceived as less severe than un-predictably directed activities (predicted directions refer mostly to on-trail activities, whereas un-predictable to off-trail, see Miller, Knight & Miller 2001; Coppes & Braunisch 2013). In addition, also the speed and/or noise of a given activity have been shown to determine its severity, where faster/louder activities

are perceived as more dangerous (Burger 1981; Arroyo & Razin 2006; Lethlean *et al.* 2017). Apart from recreational activity types, the number of recreationists (group size) in general affects the impact, with larger groups having a stronger impact (Geist *et al.* 2005; Remacha, Pérez-Tris & Delgado 2011). Finally, recreationists accompanied by dogs are perceived as more dangerous than recreationists without dogs (Miller, Knight & Miller 2001; Langston *et al.* 2007; Young *et al.* 2011; Waldstein Parsons *et al.* 2016). Even the colour of the clothing worn by the recreationist affects the threat severity (Gutzwiller & Marcum 1997; Putman *et al.* 2017).

Species characteristics

There are several species-specific characteristics which have been shown to affect the “disturbance tolerance” of an animal, e.g. nesting site, diet or body size (Blumstein *et al.* 2003; Kangas *et al.* 2010; Samia *et al.* 2015). Apart from species-specific sensitivities towards recreational activities, individual differences (e.g. sex, age or body condition) may influence human impact too. Age for example can be attributed to experience, and more experienced individuals either react stronger (sensitization) or less (habituation) towards a recreationist (but see Bejder *et al.* 2009). Animals can get used to a certain level of disturbance, but not all species, populations or individuals are able to habituate in the same way - some do habituate while others do not (Nisbet 2000; Walker, Dee Boersma & Wingfield 2006; Baudains & Lloyd 2007; Bonier, Martin & Wingfield 2007; Bejder *et al.* 2009; Rodríguez-Prieto *et al.* 2009; Samia *et al.* 2015; Vincze *et al.* 2016). This phenomenon can be seen when individuals of a certain species manage to live in human dominated urban landscapes, e.g. cities, and then fully adapt to these “artificial” environments (e.g. regardless of increased noise levels or unsuitable urban food resources (Meyrier *et al.* 2017)). Certain individuals of a given species are better capable of circumventing such new environmental hurdles, than others. These different types of

individuals are called personalities or are sometimes clustered into different reaction norms (Wilson 1998; Sih, Bell & Johnson 2004; Mathot *et al.* 2012; Sih *et al.* 2015; Nicolaus *et al.* 2016; Arroyo, Mougeot & Bretagnolle 2017), and have been attributed to affect the habituation potential (Evans, Boudreau & Hyman 2010; Rebolo-Ifrán *et al.* 2015; Cavalli *et al.* 2016; Vincze *et al.* 2016). Within urban areas (e.g. cities) one type of personality (bold, aggressive) is overrepresented compared to the homogenous distribution of personalities in a natural (rural) population (Evans, Boudreau & Hyman 2010; Miranda *et al.* 2013; Sprau & Dingemanse 2017).

Spatio-temporal context: Seasonality and habitat

Depending on the season (breeding, migration or overwintering), disturbance events can have additional far reaching consequences. When parents, for example, are hindered from feeding, their chicks will face a reduced survival, which then could have an effect up to the population level (Robert & Ralph 1975; Gładalski *et al.* 2016). During wintertime, animals flushed out of their den, face additional losses of energy, firstly due to flushing, and secondly via reduced protection from the harsh environment. This increased energy loss could lower survival (Arlettaz *et al.* 2015). When animals on migration are disturbed at stopover sites they could be forced to continue their journey without enough restored energy reserves, which lowers their survival (Pfister, Harrington & Lavine 1992). Therefore human impacts at one location can have carry-over effects on the population at an other location or in a different season (mostly for migrating species).

Besides season also the time of day when the activity takes place, influences its impact (e.g. nocturnal versus diurnal species; Tablado & Jenni 2017). Finally, also the type of habitat where a recreational activity is taking place, affects its impact. Denser vegetation shields animals from the passing recreationists (Thiel *et al.* 2007; but see also

Whittingham *et al.* 2004), whereas the disturbance impact reaches further in more open, less vegetated habitats.

Study aims

Former studies looking at human recreation impacts on wildlife were mostly comparative, and in many cases study sites had been exposed to recreation for a long time. This usually creates the following two problems: firstly there is the problem of disentangling direct from indirect effects, as they often act in combination, making it hard (or sometimes impossible) to determine the driving mechanisms. Secondly, areas already used for recreation for a while face the problem that the most sensitive species or individuals (i.e. personalities) might already have disappeared from the most heavily frequented areas (i.e. spatial rearrangement), or might have habituated to human presence, leading to animals already being “adapted” to human recreation. This can obscure the magnitude of human recreation impacts on wildlife and lead to erroneous conclusions. Therefore we used a set of well-designed comparative and experimental studies, to counteract these difficulties. We focused our studies on forest birds, as forests are a widely distributed habitat and often used for recreational activities. Birds in general are suitable for studying human recreational impacts, as they are highly mobile, quite easy to detect and census, and they show a relatively high species richness. Additionally, during breeding, most bird species are territorial and have a fixed nesting site, which facilitates catching adults and allows gathering brood data easily.

(Chapter 1) Firstly we wanted to disentangle the direct effects of humans from the indirect effects of the trails via habitat change. Therefore we compared bird communities at different distances from trails in several forests with a wide variety of human use. We used a paired point count study design, where one point count was placed close to the trail

and the second far away from the trail, to examine both human-presence and trail impact on bird communities. Moreover we investigated whether this human and/or trail impact was modulated by species specific traits.

(Chapter 2) Within the same forests, varying in human frequentation, we measured bird species-specific tolerances towards human approach using flight initiation distances (FID) in order to investigate whether birds in heavily frequented forests are already “adapted” and therefore responding less to recreation. We were examining whether FIDs of nine common forest bird species differed between forests depending on the levels of recreational use. Therefore we measured FIDs in heavily frequented forests and compared them with measures taken in an unfrequented forest.

To exclude the possibility to examine a “human-adapted” bird community, we finally focused on the least-disturbed forest and conducted two experimental studies. (Chapter 3) In the first we measured the direct impact of recreational activities on forest birds during a possibly sensitive time period, without changing the surrounding habitat. We disturbed forest plots during early-breeding season period and compared abundance and species richness of the birds which finally settled in the experimental plots with those of undisturbed control plots.

(Chapter 4) Secondly, we examined whether there are carry-over effects of the impact of human disturbance during the early-breeding season on offspring through maternal antibody deposition in the eggs during the disturbance period. A higher amount of maternal antibodies has been previously attributed to an increased survival, as the chicks fully rely on these maternal antibodies to withstand infections during the first days of their life (Pihlaja, Siitari & Alatalo 2006).

The findings of this thesis hopefully contribute to our understanding about the impact of human disturbance on wildlife and its conservation implications, in order to help us protect wildlife while allowing recreationists to appreciate nature.

CHAPTER 1

Effect of recreational trails on forest birds: does human presence matter?

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Illustration credit: Yves Bötsch

Effect of recreational trails on forest birds: does human presence matter?

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ABSTRACT

Outdoor recreational activities are increasing worldwide and occur especially close to cities at high frequency. Forests are a natural environment often used for these activities (e.g. jogging, hiking, dog walking, mountain biking, and horse riding). The pure presence of people in forests can disturb wildlife, which may perceive humans as predators. Many of these activities rely on trails, which intersect an otherwise continuous habitat and hence impact wildlife's habitat. The aim of this study was to separate the effect of the change in vegetation and habitat structure through trails, from the effect of mere human presence using these trails, on forest bird communities. Therefore we compared the effect of recreational trails on birds in two forests frequently used by recreationists with that in two rarely visited forests. In each forest, we did paired-point counts to investigate the differences between the avian community close (50m) and far (120m) from trails, while accounting for possible habitat differences. In the disturbed, high recreation level forests we found a reduction in the density of birds (-13%) and species richness (-12%) at points close to trails when compared to those further away, whereas such an effect was not detectable within the low recreation level forests. Additionally we found that the effect of human presence varied depending on the characteristics of the species. These findings

suggest that the mere presence of humans impoverishes the forest bird community along trails and affects different species differently.

Key words: Human disturbance, recreation ecology, recreational activity, avian diversity, nesting guild

INTRODUCTION

Nature-based recreational activities have increased enormously in the last decades (Boyle & Samson 1985; Steven, Pickering & Castley 2011; Monz, Pickering & Hadwen 2013; Steven & Castley 2013; Hammitt, Cole & Monz 2015). This trend is raising concerns of researchers and conservationists about the potential impact of human recreation on wild animals. Humans may be perceived by wildlife as predators (Frid & Dill 2002). Thus, when exposed to human presence, animals may react with important changes in their behaviour and physiology (e.g. increased vigilance, flight, release of stress hormones; (Ikuta & Blumstein 2003; Beale & Monaghan 2004a; b; Tablado & Jenni 2017)), which in turn might have consequences for the fitness and dynamics of animal populations.

Many studies have therefore aimed at assessing the effects of outdoor recreational activities on wildlife. One way of approaching this issue has been to investigate the effects of recreational trails on bird abundance and species composition. However, the results of these studies are not always consistent, with some studies finding an effect of trails while others do not (Gutzwiller *et al.* 1998; Miller, Knight & Miller 1998; Deluca & King 2014; Thompson 2015). One reason for this disparity could be the difficulty to disentangle the direct effect of human presence from the indirect effect of habitat modification caused by the installation of trails and roads, which entails a less dense vegetation or even the clearance of it in most habitats (Miller, Knight & Miller 1998; Miller & Hobbs 2000; Smith-Castro & Rodewald 2010; Butler *et al.* 2012; Morelli *et al.* 2015).

In order to disentangle the effects of human presence from habitat modifications through trails we examined how breeding-bird communities changed with distance to trails that were similar in size and structure, but were in forests with widely different levels of recreation. We predicted that the differences between bird communities close and far from trails will be higher in forests experiencing high recreational levels than in forests experiencing low recreational levels. That is, in high-recreation forests we expected lower

densities and richness of breeding birds close to the trails than further away, while this difference would not exist or be much lower in low-recreation forests. Additionally, we expected to find inter-specific differences in the impact of trails according to species characteristics, since habitat clearance and/or human presence are likely to affect bird species differently according to their nesting-guild, foraging-guild and sensitivity to humans (Blumstein *et al.* 2003; Langston *et al.* 2007; Mallord *et al.* 2007; Kangas *et al.* 2010; Thompson 2015).

MATERIALS AND METHODS

Study sites

We selected four different forests. Two of them (Allschwilerwald (47°32'N, 7°32'E) and Sihlwald (47°15'N, 8°33'E), in Switzerland) were close (< 2 km) to cities with more than 150,000 inhabitants, and heavily used by humans for recreation. The other two forests (Forêt de Chaux (47°05'N, 05°40'E) in France, and Laufenwald (47°26'N, 7°26'E), in Switzerland) were less frequently used (> 8 km from towns with less than 25,000 inhabitants). This classification of the forests into high and low levels of recreation through the proximity to cities was confirmed by own observations during fieldwork. In the Forêt de Chaux and Laufenwald we observed, on average, no more than one human passage per day, while there were 15-25 and 5-15 visitors per hour in the Allschwilerwald and the Sihlwald, respectively. Most recreationists were walking (with or without dogs), and a few were biking. All forests were broad-leaved, with pedunculate oaks (*Quercus robur*) and/or European beech (*Fagus sylvatica*) as the dominating tree species and some admixed European hornbeam (*Carpinus betulus*), sycamore maple (*Acer pseudoplatanus*), European ash (*Fraxinus excelsior*) and scarcely some conifer trees (*Picea abies*, *Abies alba*, *Pinus sylvestris*, *Pseudotsuga menziesii*). The four study sites contained a well-developed network of gravel roads and trails (hereafter called trails) which were freely accessible to the public for recreation (e.g. walking, biking), but where cars and motorbikes were prohibited, except for foresters.

Point count surveys

To assess the avian community near and far from trails we used classical point count surveys (Bibby *et al.* 2000) in a paired design (Fig. 1). We counted birds at 37 pairs of points within forests with a high recreational level (Allschwilerwald 8 pairs and Sihlwald 29 pairs), and at 25 pairs of points in forests with a low recreational level (Forêt de Chaux

12 pairs and Laufenwald 13 pairs). Within each pair, we placed one point close (at 50 m) to a trail and the other point further away at an average distance of 120 m (range 70 - 160 m from the trail depending on the spatial configuration). The location of the points was chosen from aerial photos, with the criterion of placing both points of a pair within a homogenous forest patch.

During each point count a single observer recorded all birds heard or seen within 50 m during six minutes. To estimate the number of territories within 50 m we used only observations of birds showing territorial behaviour (e.g. singing). We used range finders (Nikon Prostaff 7 monocular or Zeiss Victory 10x45 T* RF) to check whether observations fell inside or outside the 50 m radius. Points were censused twice in the Allschwilerwald and Sihlwald in 2013 (first round 30 May - 18 June, second round 26 June - 17 July), and three times in all four forests in 2015 (first round 18 March - 18 April, second round 18 April - 31 Mai, third round 11 May - 17 June). In 2015 we could only monitor 14 of the 29 pairs of points in the Sihlwald, due to time constraints. All point counts were done by only two observers: Y.B. in 2013 and D.S. in 2015. To account for possible researcher-related effects, the order in which points within a pair were censused changed from census round to census round. Also the order in which the pairs within a forest were censused changed from round to round to eliminate a potential effect of time of day. Point count surveys were only done in the early morning, starting right after sunrise (i.e. between 05:21 and 09:45 Central European Time (CET), (Bibby *et al.* 2000)). This means that most census work was done before the bulk of recreationists arrived (R. Schmidt unpublished data).

Vegetation surveys

In both years we recorded the vegetation to account for differences in habitat composition among points. Surveys were done at five different locations around each point (one at the point-count spot itself and four at locations 25 m away from it into the four main

cardinal directions; Fig. 1). At each location, we estimated *ground vegetation cover* (%) on a 2x2 m area, *shrub cover* (%) on a 3x3 m area (i.e. vegetation with diameter at breast height (dbh) of less than 5 cm, otherwise counted as trees) and *canopy cover* (%) by looking straight up and assessing the proportion of canopy against the sky in the visual field of the observer (same observers as for the point counts). Additionally we counted the trees on an 8x8 m area per species (*beech*, *oak* and *conifers*), including standing dead trees (*deadwood*). The vegetation surveys were conducted after the point-count censuses, when the vegetation was fully developed (end of May until September). For each vegetation variable, we averaged the vegetation measures among the five locations within each point before analysis.

Statistical analysis

In order to examine whether the avian community differed between points close to or far from trails, we used two generalized linear mixed models (GLMM), with the number of either breeding-bird territories (*Number of territories*) or breeding-bird species (*Species richness*) per point count as the dependent variable (both following a Poisson distribution). As explanatory variables we included *distance* to the trail (categorical: far vs. close), level of recreation (*disturbance*; categorical: high- vs. low level of recreation), vegetation characteristics (*ground cover*, *shrub cover*, *canopy cover*, mean number of *beech*-, *oak*-, *conifer*-trees, and dead-trees (*deadwood*)), and accounted for the seasonal and daily variation in singing-activity by including the linear and quadratic terms of the Julian date (*Jdate* and *Jdate*²), and the time (in minutes) elapsed since sunrise (Δ *Sunrise*). Vegetation variables did not show strong correlations among each other (Pearson correlation coefficient < 0.6) and were therefore all included in the models. We included the interactive effect between *distance* and *disturbance* to test for the impact of recreation on the differences between close and far points. To control for potential differences in

singing activity depending on recreation intensity (Gutzwiller *et al.* 1994; Frid & Dill 2002), we also incorporated the interaction between Δ *Sunrise* and *disturbance*. A preliminary analysis, including also trail-type, revealed, that there was no difference in effect of gravel roads versus trails (Online Resource Fig. S1). Therefore we removed trail-type as variable from further analyses. As random factors we included *year*, which accounted for both the inter-annual differences in bird community and observer effect (observer changed with year), *round* (to control for correlations among counts within the same census period), and *point_ID* nested within *pair_ID*, which in turn was nested within *Site*, to account for spatial autocorrelation (Table 1).

In order to explore differences in response to trails according to species properties, we performed three additional GLMMs. These had a similar structure as the previous ones but additionally included either a three-level factor describing *nesting-guild* (cavity, ground or open-cup nesters according to Perrins and Cramp (1998)), a two-level factor describing *foraging-guild* (ground vs. above-ground according to Perrins and Cramp (1998)) or a two-level factor describing the *sensitivity* towards humans, respectively, as well as their two-way and three-way interactions with *distance* and *disturbance*. In order to define sensitivity towards humans we used the species' mean flight initiation distance (FID) (low sensitivity = FID lower than the median FID for all our species vs. high sensitivity = FID equal or larger than the median FID; FID data from Møller (2008) and Díaz *et al.* (2013) for non-urban areas; see Online Resource Table S1). We acknowledge that FID may be modulated by many factors (Tablado & Jenni 2017), but is still a reasonable and widely available proxy for sensitivity to human disturbance (Blumstein *et al.* 2003).

All analyses were conducted in R version 3.3.0 (Ihaka & Gentleman 1996; R Core Team 2016) using the *glmer* function from the R-package *lme4* (Bates *et al.* 2015). For calculating the 95% credible intervals (CrI) of the model estimates we used the Bayesian framework (function *sim* from the R-package *arm* (Gelman & Su 2015)), simulating 10,000

random samples of the joint posterior distribution of the model parameters (Online Resource Fig. S2). Additionally, we computed the pairwise differences (with 95% CrI) of the number of territories and species between close and far points (Figs. 2 and 3) using the highest probability density interval-function (HPDInterval-function from the R-package coda; (Plummer *et al.* 2006)). For all models we evaluated whether model assumptions were fulfilled, via analysis of the residuals and checking for overdispersion after Korner-Nievergelt *et al.* (2015). To facilitate model convergence all numeric explanatory variables were centred and standardized (mean = 0, sd = 1).

RESULTS

In forests with a high level of recreation the number of territories at points close to trails was 12.9 % lower than at paired points further away (7.2 versus 8.3 territories on average), while in forests with a low level of recreation no difference between points close to and far from trails was noticeable (7.9 versus 7.8 on average) (Fig. 2a, Table 1). Similarly, we found a reduction of 12.0 % for species richness (5.7 species versus 6.5 on average) at points close to trails compared to far points in forests with a high level of recreation, which was not observed in forests with low levels of recreation (6.4 species in both on average) (Fig. 2b, Table 1). Additionally, we found a quadratic effect of Julian date on the number of territories. That is, records of breeding-bird territories were more numerous in the middle of the season compared to early or late spring, which reflects the general singing phenology of breeding birds. Furthermore, the number of oaks positively affected the number of territories and species richness, while the number of beeches negatively affected the number of territories (Table 1).

Cavity nesters (and to a certain extent also open-cup nesters) had lower numbers of territories and species close to trails compared to paired points further away in forests with high levels of recreation (Figs. 3a and b, Online Resource Table S2 and Figs. S2a and b). This effect was not observed in forests with low levels of recreation, where proximity to trails seems to only slightly decrease cavity nester presence (Figs. 3a and b, Online Resource Table S2 and Figs. S2a and b). Ground-nesting birds, on the other hand, showed higher numbers of territories and species close to trails than far from them in forests with low levels of recreation (Figs. 3a and b, Online Resource Table S2 and Figs. S2a and b). However, this positive effect of trails was not observed in forests with high levels of recreation. The foraging-guild specific analysis revealed no differences in number of territories or species between close and far points in forests with low levels of recreation, whereas in forests with a high level of recreation, above-ground foragers

showed a reduction in number of territories and species close to trails compared to further away (Figs. 3c and d, Online Resource Table S3 and Figs. S2c and d). Concerning sensitivity to humans, we found that in forests with high levels of recreation both high- and low- sensitivity species showed lower numbers of territories, and to a certain extent also of species, close to versus far from trails. In forests with a low level of recreation, however, the tendency of lower numbers of territories and species close to trails was less important and only observed in highly sensitive species (Figs. 3e and f, Online Resource Table S4 and Figs. S2e and f).

DISCUSSION

In this study, we were able to disentangle the effect of human presence from that of trail-associated habitat modifications by investigating the response of the avian community to trails with different levels of recreation. We showed that the disturbance caused by recreation activities (mostly walking) reduced forest bird density and richness by 12 - 13% and that this effect was not merely due to the habitat modification associated with the presence of trails. This agrees with an experimental study with humans walking off-trail in a forest in France where it was observed that humans *per se*, without habitat modification, negatively impact the bird community (Bötsch *et al.* unpubl. data). Our findings are also comparable to those of Ware *et al.* (2015) who found that traffic-noise alone, without real roads, was enough to cause a reduction in bird density.

Habitat modifications resulting from trail construction may have a positive or negative effect depending on bird species (Morelli *et al.* 2014). We found a positive influence of trails on the number of ground nesting birds (Figs. 3a and b for low-recreation forests), although this positive effect disappeared with disturbance in forests with a high level of recreation. This could be explained by the fact that forest clearing for trail construction allows the development of a rich understory at the edges, which in turn can serve as refuge and breeding-site/nest cover for ground nesters (Virkkala 1987; Trzcinski, Fahrig & Merriam 1999; Šálek, Svobodová & Zasadil 2010). Conversely, for cavity nesters there was a tendency, although small, to fewer territories and species close to trails even in forests with low levels of recreation. This could be due to the clearing of old, large trees (which provide natural cavities) during trail construction and also later for visitor safety reasons. The effect of trails *per se* is also in agreement with previous studies in tropical forests, where trail construction has been suggested to impact bird communities negatively (Andrén 1994; Laurance, Stouffer & Laurence 2004; Laurance, Goosem & Laurance 2009). The importance of habitat in driving avian community is further confirmed in our

analyses by the overall positive effect of oaks on both the number of territories and species richness, which coincides with previous studies which show that oaks are determinants of forest biodiversity (Caprio, Ellena & Rolando 2009).

The impact of recreational trails also varied according to other species characteristics, such as, foraging guild and sensitivity to humans. Surprisingly, we did not find a strong effect of recreational trails on ground foragers as we expected after Thompson (2015). This could be due to the overall low number of ground foragers found in these forests or the higher availability of food along the trail edge for certain species (Šálek, Svobodová & Zasadil 2010; Batáry *et al.* 2014). Highly sensitive species (large FID) seem to avoid areas close to trails even in forests with low levels of recreation, while low-sensitivity species seem to only be negatively affected by trail presence in highly frequented forests. Therefore sensitivity, approximated by FID, as we did, could be used to help designing future conservation measures through management of tourist numbers and access (Blumstein *et al.* 2003, 2005; Fernández-Juricic *et al.* 2005; Koch & Paton 2014).

In conclusion, by comparing the response of the bird community to trails in high-recreation versus low-recreation forests, we observed that human presence *per se* causes important disturbance to birds in recreational areas and that the overall effect of recreational trails depends not only on recreation intensity but also on species characteristics. Moreover, the fact that we found a negative effect of recreationists on the avifauna of forests which have been used for recreation for decades suggests that habituation to humans has not been able to outweigh the negative impact of human disturbance. Our findings have also some additional implications. Firstly, census and monitoring schemes which are often done from roads and trails (Hanowski & Niemi 1995; Sutter, Devis & Duncan 2000; Sauer *et al.* 2013) should take into account the species-specific responses to habitat alterations and the level of recreation on trails in order to interpret the census results adequately. Secondly, our results provide further evidence that

the impact of recreation could be reduced by limiting the access of visitors to certain areas (core wilderness areas) and encouraging visitors to stay on trails elsewhere (Miller, Knight & Miller 2001; Reed & Merenlender 2008; Coppes & Braunisch 2013). Enough undisturbed wildlife habitat (quiet zones) away from trails not only benefits birds, but also mammals (Taylor & Knight 2003; George & Crooks 2006; Reed & Merenlender 2008). Finally, if new recreational trails or roads have to be constructed a well-designed plan is crucial, which incorporates habitat and spatial requirements of the different species (e.g. sensitivity to humans or fragmentation; Andrén 1994; Reed et al. 1996; Forman and Alexander 1998; Rodríguez-Prieto et al. 2014), considers renaturation of unused trails (e.g. harvesting roads) and takes into account the possibility that new trails facilitate access of new predators (Miller & Hobbs 2000). In summary, this study supports that trails and roads can profoundly affect bird community composition and abundance, not only by modifying habitat along trails, but mainly through their use by recreationists.

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TABLES

Table 1 Model estimates (\pm 95% CrI) of the effects tested in the GLMMs investigating the impact of recreational trails on the overall number of territories and species richness. The corresponding level of each factor is given in parentheses after the variable name. The missing factor levels are the ones used as reference categories in the models

Dependent variable	Number of territories	Species richness
Intercept	2.070 (1.604; 2.516)	1.856 (1.568; 2.147)
Distance (far)	-0.012 (-0.116; 0.090)	-0.003 (-0.124; 0.121)
Disturbance (high)	-0.092 (-0.216; 0.035)	-0.116 (-0.274; 0.039)
Julian date	0.100 (0.042; 0.159)	0.018 (-0.046; 0.084)
Julian date ²	-0.045 (-0.086; -0.004)	-0.042 (-0.088; 0.071)
Δ Sunrise	0.018 (-0.039; 0.074)	0.005 (-0.060; 0.071)
Ground cover	0.009 (-0.032; 0.051)	0.007 (-0.040; 0.056)
Shrub cover	0.019 (-0.015; 0.054)	0.025 (-0.017; 0.065)
Canopy cover	-0.005 (-0.050; 0.041)	-0.006 (-0.060; 0.049)
Beeches	-0.050 (-0.092; -0.008)	-0.047 (-0.096; 0.001)
Oaks	0.042 (0.004; 0.081)	0.047 (0.003; 0.091)
Conifers	-0.026 (-0.071; 0.019)	-0.023 (-0.075; 0.029)
Deadwood	-0.014 (-0.053; 0.025)	-0.003 (-0.046; 0.042)
Δ Sunrise \times Disturbance (high)	0.013 (-0.059; 0.085)	0.017 (-0.067; 0.099)
Disturbance (high) \times Distance (far)	0.150 (0.015; 0.285)	0.130 (-0.024; 0.286)

Distribution = Poisson; link function = natural logarithm; random factors = year, round, and point_ID/pair_ID/Site

FIGURES

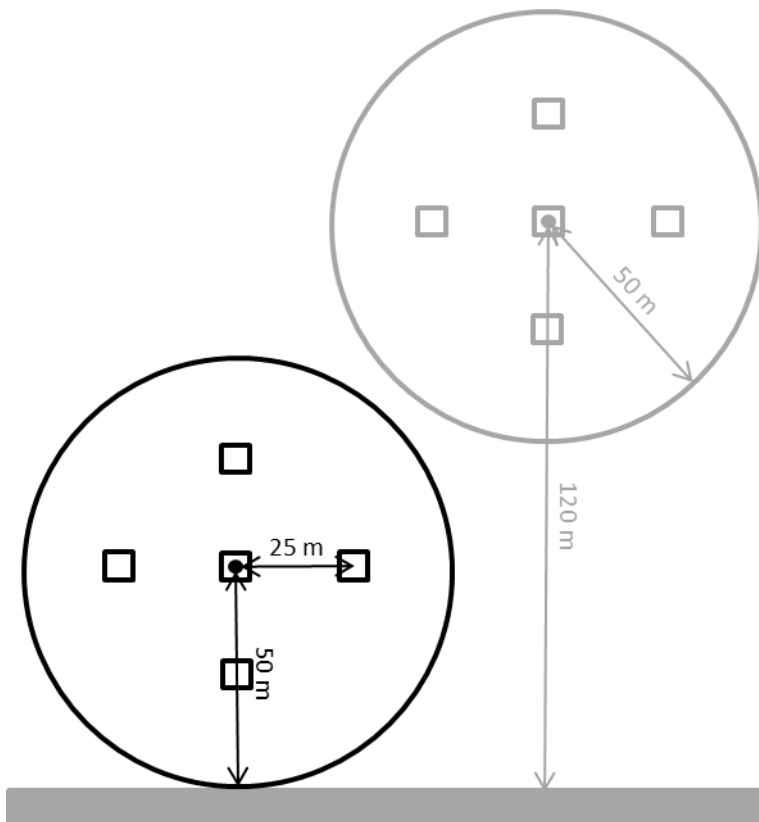


Fig. 1 Schematic representation of a pair of points for counting birds within a radius of 50m (circles). The grey bar represents a trail. The black and grey circles represent the surveyed area of the point close and far from the trail, respectively. Squares (five in each point count circle) show the locations where the vegetation survey took place. The middle point is the spot from which the bird census (point count) was performed

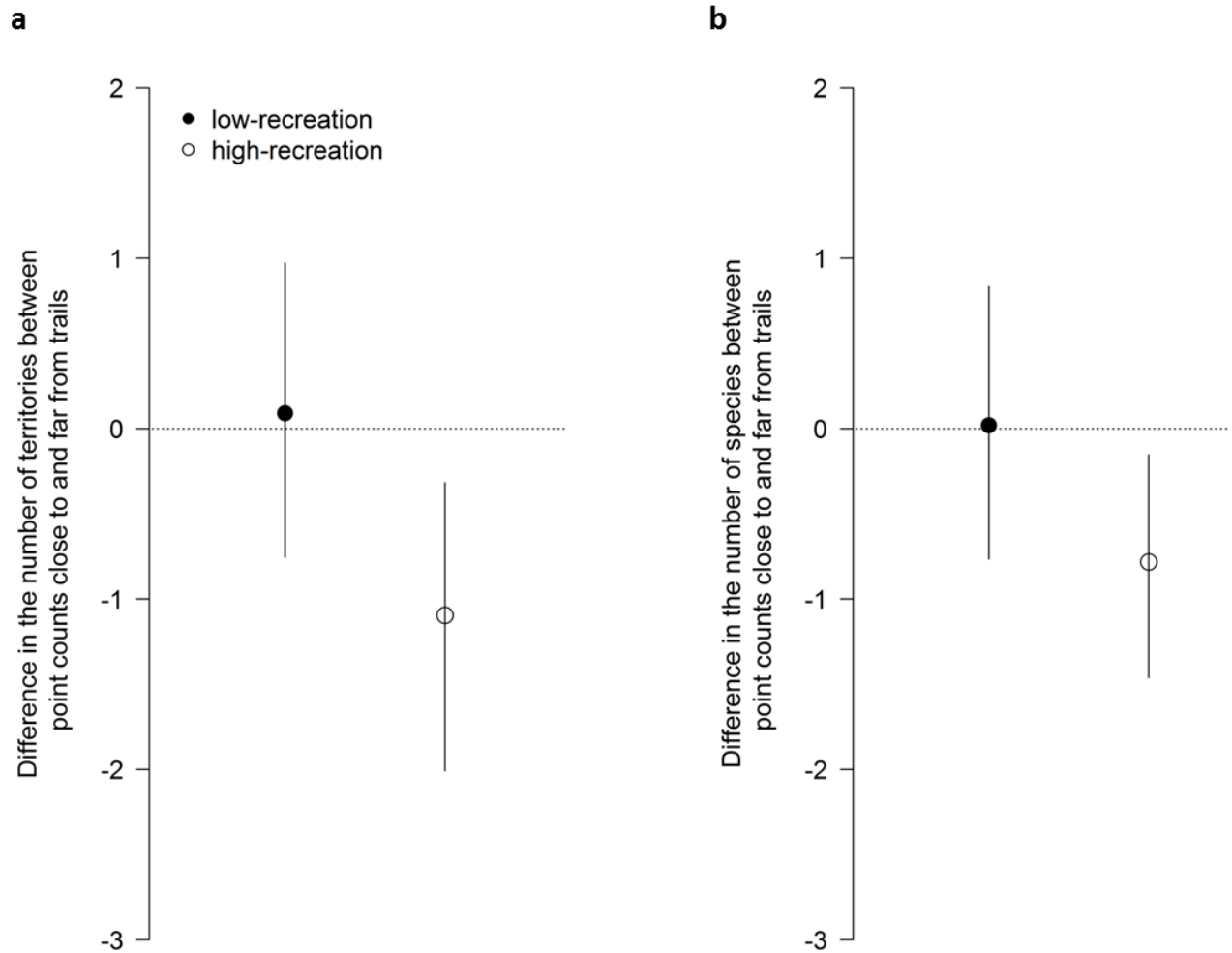


Fig. 2 Differences (mean \pm 95% CrI) in the fitted number of territories (a) and species (b) between paired point-counts close to and far from trails in forests with low- or high- levels of recreation. Negative values indicate more territories or species far from trails while positive values indicate higher number of territories or species closer to trails. The dotted line (zero) represents an equal number of territories or species at both distances from the trail

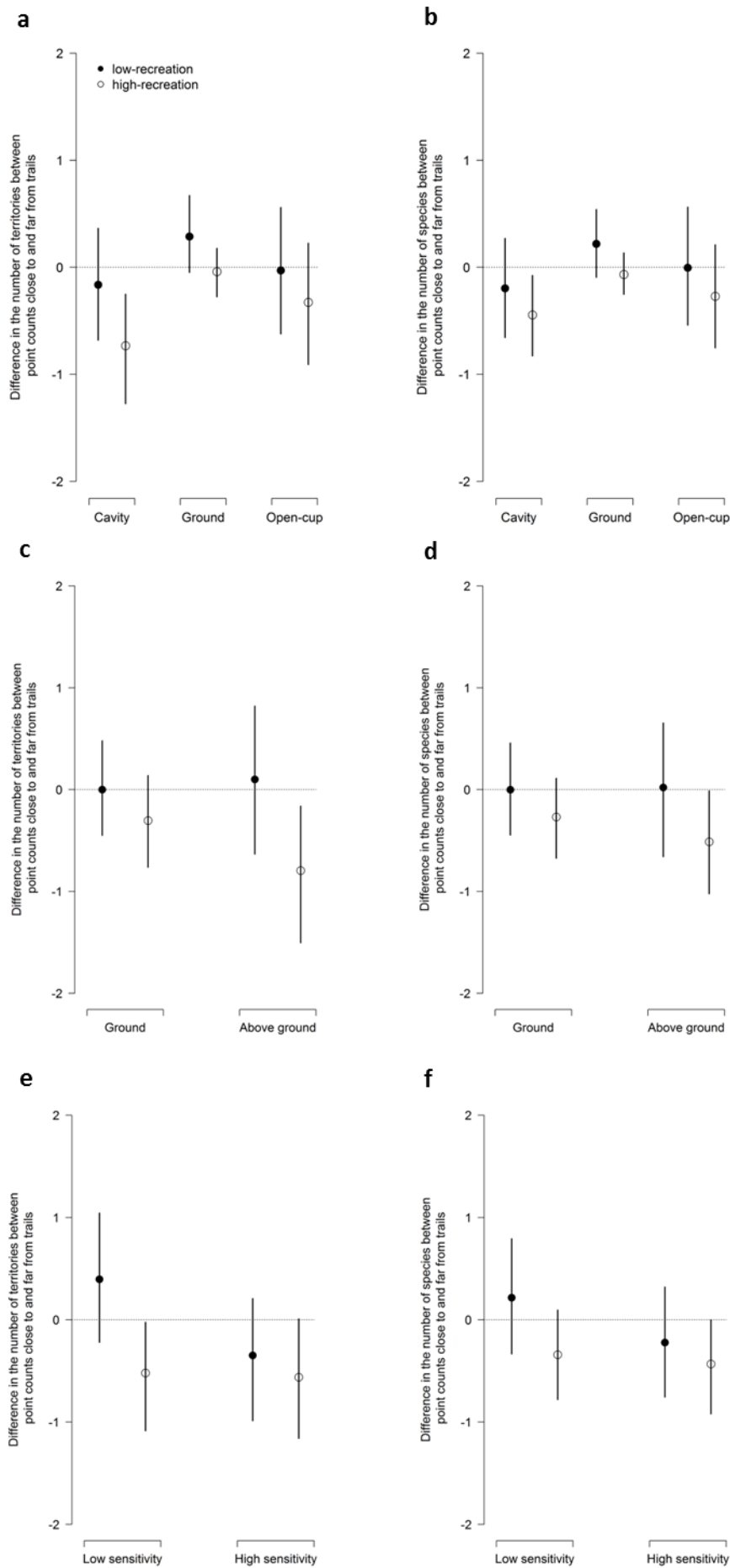


Fig. 3 Mean differences ($\pm 95\%$ CI) in the fitted number of territories and species, respectively, between points close and far from trails in forests with high- and low levels of recreation, according to (a, b) nesting-guild, (c, d) foraging-guild, and (e, f) sensitivity towards humans. Negative values indicate more territories or species per guild at far points compared to close points, positive values indicate the opposite, while the dotted line represents an equal number between far and close points

Online Resource

Table S1 List of bird species recorded during the censuses in 2013 and 2015, with scientific and English names, corresponding nesting-guild, foraging-guild and classification into two sensitivity groups (according to flight initiation distance (FID): High = FID \geq median FID, Low = FID < median FID, median FID = 12.85m)

Scientific name	English name	Nesting guild ¹	Foraging guild ¹	Sensitivity ²
<i>Accipiter nisus</i>	Eurasian Sparrowhawk	Open-cup	Above ground	High
<i>Aegithalos caudatus</i>	Long-tailed Tit	Open-cup	Above ground	Low
<i>Buteo buteo</i>	Common Buzzard	Open-cup	Above ground	High
<i>Certhia brachydactyla</i>	Short-toed Treecreeper	Open-cup	Above ground	Low
<i>Certhia familiaris</i>	Eurasian Treecreeper	Open-cup	Above ground	Low
<i>Coccothraustes coccothraustes</i>	Hawfinch	Open-cup	Above ground	High
<i>Columba oenas</i>	Stock Dove	Cavity	Ground	High
<i>Columba palumbus</i>	Common Wood Pigeon	Open-cup	Ground	High
<i>Cuculus canorus</i>	Common Cuckoo	Open-cup	Above ground	High
<i>Cyanistes caeruleus</i>	Eurasian Blue Tit	Cavity	Above ground	Low
<i>Dendrocopos major</i>	Great Spotted Woodpecker	Cavity	Above ground	High
<i>Dendrocopos medius</i>	Middle Spotted Woodpecker	Cavity	Above ground	-
<i>Dryocopus martius</i>	Black Woodpecker	Cavity	Above ground	High
<i>Emberiza citrinella</i>	Yellowhammer	Ground	Ground	Low
<i>Erithacus rubecula</i>	European Robin	Ground	Ground	Low
<i>Ficedula hypoleuca</i>	European Pied Flycatcher	Cavity	Above ground	Low
<i>Fringilla coelebs</i>	Common Chaffinch	Open-cup	Above ground	High
<i>Garrulus glandarius</i>	Eurasian Jay	Open-cup	Above ground	High
<i>Lophophanes cristatus</i>	European Crested Tit	Cavity	Above ground	Low
<i>Muscicapa striata</i>	Spotted Flycatcher	Open-cup	Above ground	Low
<i>Oriolus oriolus</i>	Eurasian Golden Oriole	Open-cup	Above ground	High
<i>Parus major</i>	Great Tit	Cavity	Above ground	Low
<i>Pariparus ater</i>	Coal Tit	Cavity	Above ground	Low
<i>Phylloscopus bonelli</i>	Western Bonelli's Warbler	Ground	Above ground	Low
<i>Phylloscopus collybita</i>	Common Chiffchaff	Ground	Above ground	Low
<i>Phylloscopus sibilatrix</i>	Wood Warbler	Ground	Above ground	-
<i>Phylloscopus trochilus</i>	Willow Warbler	Ground	Above ground	Low
<i>Picus canus</i>	Grey-headed Woodpecker	Cavity	Ground	High
<i>Picus viridis</i>	European Green Woodpecker	Cavity	Ground	High
<i>Poecile montanus</i>	Willow Tit	Cavity	Above ground	Low
<i>Poecile palustris</i>	Marsh Tit	Cavity	Above ground	Low
<i>Prunella modularis</i>	Dunnock	Open-cup	Ground	Low
<i>Pyrrhula pyrrhula</i>	Eurasian Bullfinch	Open-cup	Above ground	Low
<i>Regulus regulus</i>	Goldcrest	Open-cup	Above ground	Low
<i>Rgulus ignicapilla</i>	Common Firecrest	Open-cup	Above ground	Low
<i>Sitta europaea</i>	Eurasian Nuthatch	Cavity	Above ground	High
<i>Streptopelia turtur</i>	European Turtle Dove	Open-cup	Ground	High

<i>Strix aluco</i>	Tawny Owl	Cavity	Above ground	-
<i>Sturnus vulgaris</i>	Common Starling	Cavity	Ground	High
<i>Sylvia atricapilla</i>	Eurasian Blackcap	Open-cup	Above ground	High
<i>Troglodytes troglodytes</i>	Eurasian Wren	Open-cup	Ground	Low
<i>Turdus merula</i>	Common Blackbird	Open-cup	Ground	High
<i>Turdus philomelos</i>	Song Trush	Open-cup	Ground	High
<i>Turdus pilaris</i>	Fieldfare	Open-cup	Ground	High
<i>Turdus viscivorus</i>	Mistle Thrush	Open-cup	Ground	High

¹: Perrins & Cramp 1998, ²: Diaz et al. 2013, Møller 2008 ; - no data available

Table S2 Model estimates (\pm 95% CrI) of the determinants of number of territories and species in the nesting-guild-specific GLMMs. The corresponding factor categories are given in parenthesis. The missing categories are used as reference in the models

Dependent variable	Number of territories	Species richness
Intercept	1.029 (0.548; 1.492)	0.767 (0.455; 1.090)
Distance (far)	0.055 (-0.113; 0.224)	0.088 (-0.115; 0.293)
Disturbance (high)	-0.316 (-0.507; -0.132)	-0.210 (-0.435; 0.009)
Juliandate	0.100 (0.041; 0.160)	0.018 (-0.047; 0.084)
Juliandate ²	-0.045 (-0.086; -0.004)	-0.042 (-0.087; 0.004)
Δ Sunrise	0.018 (-0.040; 0.074)	0.005 (-0.060; 0.072)
Ground cover	0.009 (-0.033; 0.051)	0.007 (-0.041; 0.057)
Shrub cover	0.019 (-0.015; 0.054)	0.024 (-0.015; 0.066)
Canopy cover	-0.004 (-0.050; 0.041)	-0.005 (-0.060; 0.048)
Beeches	-0.050 (-0.092; -0.008)	-0.048 (-0.097; 0.003)
Oaks	0.041 (0.003; 0.080)	0.047 (0.003; 0.090)
Conifers	-0.026 (-0.070; 0.019)	-0.023 (-0.076; 0.029)
Deadwood	-0.015 (-0.053; 0.025)	-0.003 (-0.047; 0.043)
Nesting-guild (ground)	-0.712 (-0.918; -0.505)	-0.647 (-0.894; -0.400)
Nesting-guild (open-cup)	0.296 (0.138; 0.454)	0.368 (0.185; 0.554)
Δ Sunrise \times Disturbance (high)	0.014 (-0.059; 0.086)	0.016 (-0.065; 0.100)
Disturbance (high) \times Distance (far)	0.246 (0.013; 0.471)	0.137 (-0.132; 0.405)
Distance (far) \times Nesting-guild (ground)	-0.285 (-0.590; 0.010)	-0.300 (-0.666; 0.059)
Distance (far) \times Nesting-guild (open-cup)	-0.047 (-0.267; 0.169)	-0.087 (-0.349; 0.171)
Disturbance (high) \times Nesting-guild (ground)	-0.348 (-0.657; -0.034)	-0.455 (-0.811; -0.095)
Disturbance (high) \times Nesting-guild (open-cup)	0.495 (0.285; 0.706)	0.288 (0.039; 0.534)
Distance (far) \times Disturbance (high) \times Nesting-guild (ground)	0.036 (-0.402; 0.479)	0.183 (-0.328; 0.689)
Distance (far) \times Disturbance (high) \times Nesting-guild (open-cup)	-0.185 (-0.473; 0.106)	-0.063 (-0.402; 0.280)

Distribution = Poisson; link function = natural logarithm; random factors = year, round, and point_ID/pair_ID/Site

Table S3 Model estimates (\pm 95% CrI) of the determinants of number of territories and species in the foraging-guild-specific GLMMs with corresponding factor categories given in parenthesis. The missing factor levels are the ones used as reference in the models

Dependent variable	Number of territories	Species richness
Intercept	0.848 (0.380; 1.323)	0.724 (0.104; 1.039)
Distance (far)	0.003 (-0.188; 0.188)	0.002 (-0.205; 0.212)
Disturbance (high)	0.121 (-0.068; 0.310)	0.075 (-0.142; 0.290)
Juliandate	0.099 (0.043; 0.159)	0.019 (-0.048; 0.083)
Juliandate ²	-0.045 (-0.086; -0.005)	-0.042 (-0.087; 0.003)
Δ Sunrise	0.018 (-0.039; 0.075)	0.005 (-0.061; 0.071)
Ground cover	0.009 (-0.031; 0.051)	0.007 (-0.041; 0.055)
Shrub cover	0.020 (-0.015; 0.054)	0.025 (-0.015; 0.066)
Canopy cover	-0.005 (-0.050; 0.041)	-0.006 (-0.060; 0.048)
Beeches	-0.050 (-0.091; -0.009)	-0.048 (-0.096; 0.001)
Oaks	0.042 (0.004; 0.080)	0.047 (0.005; 0.090)
Conifers	-0.026 (-0.071; 0.020)	-0.023 (-0.074; 0.028)
Deadwood	-0.014 (-0.052; 0.026)	-0.002 (-0.047; 0.043)
Foraging-guild (above ground)	0.869 (0.712; 1.023)	0.750 (0.576; 0.929)
Δ Sunrise \times Disturbance (high)	0.013 (-0.060; 0.086)	0.017 (-0.067; 0.098)
Disturbance (high) \times Distance (far)	0.105 (-0.134; 0.337)	0.110 (-0.150; 0.371)
Distance (far) \times Foraging-guild (above ground)	-0.019 (-0.242; 0.207)	-0.003 (-0.259; 0.247)
Disturbance (high) \times Foraging-guild (above ground)	-0.314 (-0.519; -0.113)	-0.297 (-0.530; -0.073)
Distance (far) \times Disturbance (high) \times Foraging-guild (above ground)	0.068 (-0.212; 0.354)	0.027 (-0.296; 0.351)

Distribution = Poisson; link function = natural logarithm; random factors = year, round, and point_ID/pair_ID/Site

Table S4 Model estimates (\pm 95% CrI) of the determinants of number of territories and species in the sensitivity-specific GLMMs. The corresponding factor levels are given in parenthesis next to the variable name whereas the missing levels are the ones used as reference in the models

Dependent variable	Number of territories	Species richness
Intercept	1.431 (0.964; 1.890)	1.198 (0.899; 1.483)
Distance (far)	-0.098 (-0.242; 0.047)	-0.066 (-0.234; 0.102)
Disturbance (high)	-0.265 (-0.420; -0.109)	-0.196 (-0.382; -0.009)
Juliandate	0.093 (0.034; 0.152)	0.009 (-0.058; 0.076)
Juliandate ²	-0.044 (-0.084; -0.003)	-0.042 (-0.087; 0.004)
Δ Sunrise	0.024 (-0.031; 0.081)	0.010 (-0.055; 0.075)
Ground cover	0.009 (-0.032; 0.051)	0.008 (-0.040; 0.056)
Shrub cover	0.023 (-0.012; 0.059)	0.027 (-0.014; 0.067)
Canopy cover	-0.005 (-0.051; 0.042)	-0.008 (-0.062; 0.047)
Beeches	-0.044 (-0.085; -0.003)	-0.041 (-0.090; 0.008)
Oaks	0.047 (0.010; 0.085)	0.051 (0.008; 0.093)
Conifers	-0.021 (-0.066; 0.023)	-0.018 (-0.069; 0.035)
Deadwood	-0.017 (-0.056; 0.022)	-0.004 (-0.050; 0.041)
Sensitivity (high)	-0.174 (-0.317; -0.032)	-0.113 (-0.282; 0.053)
Δ Sunrise \times Disturbance (high)	0.006 (-0.064; 0.078)	0.011 (-0.072; 0.093)
Disturbance (high) \times Distance (far)	0.242 (0.048; 0.437)	0.184 (-0.037; 0.405)
Distance (far) \times Sensitivity (high)	0.191 (-0.015; 0.393)	0.137 (-0.099; 0.375)
Disturbance (high) \times Sensitivity (high)	0.393 (0.202; 0.585)	0.205 (-0.017; 0.423)
Distance (far) \times Disturbance (high) \times Sensitivity (high)	-0.208 (-0.471; 0.065)	-0.122 (-0.433; 0.188)

Distribution = Poisson; link function = natural logarithm; random factors = year, round, and point_ID/pair_ID/Site

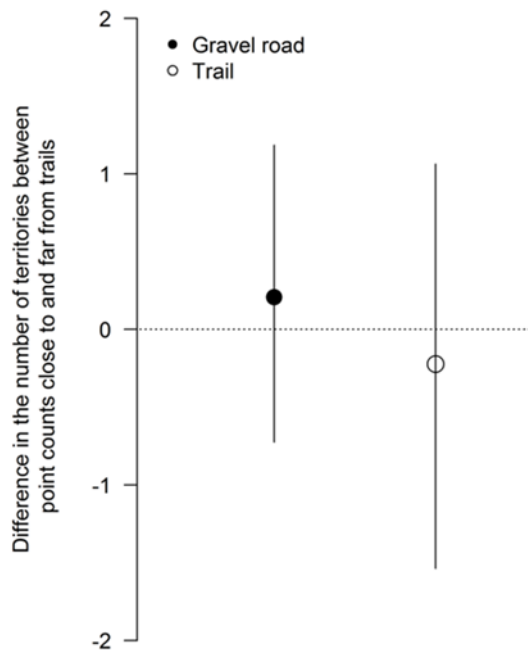
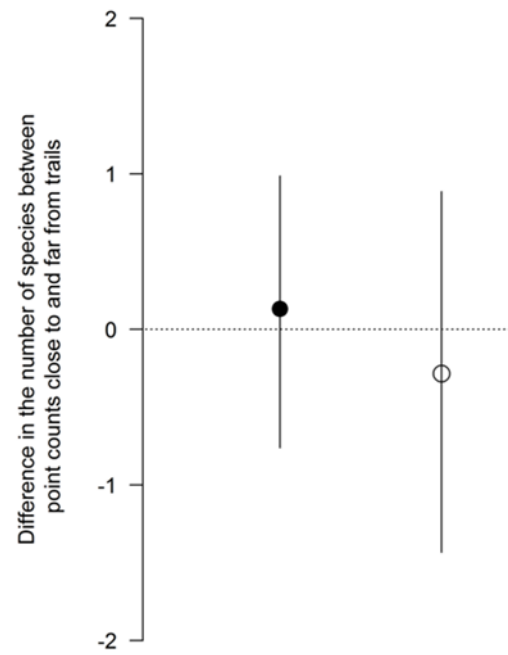
a**b**

Fig. S1 Mean differences (\pm 95% CrI) in number of territories (a) or species (b) between close and far points within forests with a low level of recreation, when considering the path type (Trails versus gravel roads)

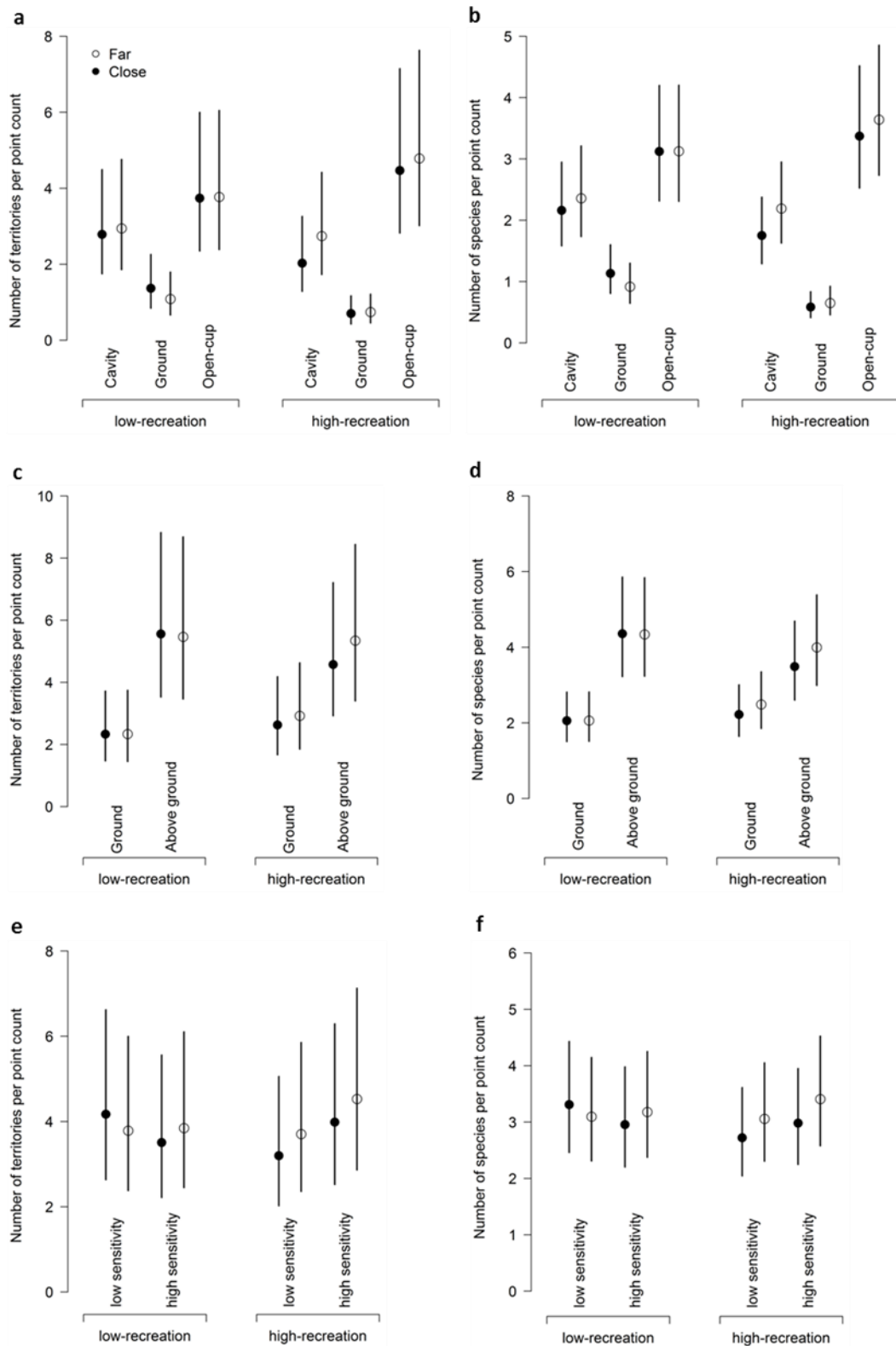


Fig. S2 Number (mean \pm 95% CrI) of territories and species, respectively, between close and far points for low- and high-recreation forests for: (a) and (b) nesting-guilds, (c) and (d) foraging-guilds, and (e) and (f) sensitivity towards humans

CHAPTER 2

Effect of human recreation on bird anti-predatory response

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Illustration credit: Yves Bötsch

Effect of human recreation on bird anti-predatory response

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Abstract

Wildlife perceives humans as predators, and therefore normally flushes. Flight initiation distance (FID), is the distance a human can approach an animal on steady pace until it flushes. Recently several studies showed differences in within-species FID between urban and rural habitats, with urban birds showing reduced FID. However, urban and rural habitats also differ in structure which might affect FID. Therefore, we investigated whether differences in FID are also present in natural habitats (forests) differing only in the intensity of human use for recreation. We found distinctly shorter FIDs in forests used intensely by humans than in a forest hardly frequented by humans. Whether this finding is driven by non-random settlement of different personalities or phenotypic plasticity (habituation-potential) cannot be assessed with our data. Studies relying on FIDs should also incorporate human recreation intensity, as this affects the measurements strongly.

Key words: Flush distance, escape distance, human disturbance, habituation

INTRODUCTION

Human disturbance through recreational activities has recently been found to negatively affect wildlife (Thiel *et al.* 2007; Kangas *et al.* 2010; Coppes *et al.* 2017; Bötsch, Tablado & Jenni 2017). To protect wild animals from the negative effects of recreation, zones with restricted access or buffer zones around breeding areas are a widely recommended mitigation measure (Rodgers & Smith 1995; Fernández-Juricic, Jimenez & Lucas 2001; Blumstein *et al.* 2003; Ikuta & Blumstein 2003). To define buffer zones an appropriate set-back distance, matching the focal species needs, has to be chosen. Unfortunately conservation measures often have to be defined quickly and ad hoc, without time for area-specific in-depth studies. Often the so called flight initiation distance (FID) has been used to define a minimal set-back distance. FID is the distance at which humans can approach a species before triggering its anti-predatory/escape behaviour. FIDs have been used widely for decades and still are considered a good surrogate for set-back distances (Samia *et al.* 2017). Many modulating factors have been found to affect these FIDs (Gutzwiller & Marcum 1997; Eason *et al.* 2006; Thiel *et al.* 2007; Carrete & Tella 2010; Legagneux & Ducatez 2013; Cavalli *et al.* 2016; Wilson-Aggarwal *et al.* 2016; Lethlean *et al.* 2017). There are intrinsic differences between species and individuals (Blumstein *et al.* 2003; Carrete & Tella 2010), but also many habitat- and context-specific effects have been reported, such as shorter FIDs in denser habitats (Tablado & Jenni 2017). Recently, studies have shown differences in bird tolerance to human approach across an urban-rural gradient, with urban populations showing reduced FIDs compared to rural conspecifics (McGiffin *et al.* 2013; Møller *et al.* 2013; Cavalli *et al.* 2016). These reduced FIDs have been attributed to habituation to humans and/or the selection of human-tolerant individuals (personalities) in urban environments (McGiffin *et al.* 2013; Cavalli *et al.* 2016; Vincze *et al.* 2016; Samia *et al.* 2017; Sprau & Dingemanse 2017). These studies demonstrate an effect of highly anthropogenic environments on bird escape

reactions. However, urban and rural habitats also differ in habitat structure which might affect FID (Whittingham *et al.* 2004; Thiel *et al.* 2007), and rural habitats may also be frequented strongly by humans. Therefore it remains unclear whether the differences in FIDs between urban and rural environments are due to differences between habitats or the frequency of humans. Moreover, little is known about the effect of lower levels of human presence, such as that occurring during recreation in natural areas, on bird anti-predatory behaviour.

Therefore, the aim of this study was to investigate whether FIDs of birds in forests near large urban settlements, and thus often frequented by humans, differ from bird FIDs in rarely visited forests of similar structure.

MATERIALS AND METHODS

Study sites

We measured FIDs in three different forests, two of which were close to cities (the “Allschwilerwald” near Basel (193,000 inhabitants), Switzerland, 47°32’N 7°32’E and the “Sihlwald” near Zurich (415,000 inhabitants), Switzerland, 47°16’N 8°33’E) and therefore heavily frequented by humans, and one forest where human recreation occurred at a very low level (“Forêt de Chaux” >9km from Dole (23,000 inhabitants), Département du Franche-Comté, France, 47°5’N 5°41’E). These forests were all deciduous and fully free to access for people. The Allschwilerwald and the Forêt de Chaux are both dominated by pedunculate oak (*Quercus robur*) whereas the Sihlwald mainly consists of European beech (*Fagus sylvatica*). In 2015 we measured FIDs in the “Forêt de Chaux”, whereas in 2016 we measured FIDs in all three forests.

FID-measures

As the vegetation density affects visibility (detection of humans by birds), and therefore also FID, we took FID measures only in early spring, from the beginning of March until the end of April, to avoid the foliated season. By measuring FIDs only in these two months we were also reducing the noise caused by variations in antipredatory-responses across life-history stages. To be able to approach birds on a straight line at steady pace, we selected rather open forest areas, with a poor shrub layer but a closed canopy (for forest details see also Bötsch et al. in prep). To obtain a sufficient sample size we focused on a few common species: common blackbird (*Turdus merula*), common chaffinch (*Fringilla coelebs*), Eurasian nuthatch (*Sitta europaea*), European robin (*Erithacus rubecula*), great tit (*Parus major*), marsh tit (*Poecile palustris*), short-toed treecreeper (*Certhia brachydactyla*), song thrush (*Turdus philomelos*) and winter wren (*Troglodytes troglodytes*).

FID was measured by a single person approaching a located bird, that did not yet react visibly to our presence (e.g. by alert posture or alarm calling), at steady pace. Only single birds, either singing, feeding or resting were measured, as birds on a nest or birds in groups have been shown to flush differently (Fernández-Juricic, Jimenez & Lucas 2002). FID was measured with range finding binoculars (ZEISS Victory 10x45 T* RF) as the horizontal line between the observer and the tree, bush or ground where the bird was before flushing. We also measured the height above ground where the bird was sitting as well as the distance at which the measuring person discovered the individual (starting distance) (Blumstein 2003).

Data analysis

We applied a generalized linear mixed model using the lme4-package in R v. 3.3.0 (Bates *et al.* 2015; R Core Team 2016).

We included as explanatory variables: starting distance, height above ground, time of day (daytime), Julian date, species, recreation level (low or highly frequented forest), and the interaction between species and recreation. All continuous variables were standardised to facilitate model convergence (mean=0, sd=1). We included year and observer as random factors to account for variability among years and the five observers. To account for phylogenetic relatedness between the species, we included the family of each species as random factor into the model. We visually checked for the goodness of fit by plotting residuals.

For making inference we used a Bayesian approach (after Korner -Nievergelt *et al.* (Korner-Nievergelt *et al.* 2015)). We simulated 10,000 random samples from the posterior distribution by using the sim-function from the R-package arm (Gelman & Su 2015). From these random samples we used the 2.5 % and 97.5 % quantiles as the limits of the 95 % credible interval (CrI). To be able to investigate species-specific differences between the

forests, we computed posterior probabilities (PP). PPs describe the probability that the difference in FID (for a given species) between two forests is different from zero: PPs can take values between 0.5 (no difference) and 1 (different).

RESULTS

For each species we had the following FID sample sizes: 73 for common blackbird, 121 for common chaffinch, 62 for Eurasian nuthatch, 94 for European robin, 132 for great tit, 39 for marsh tit, 23 for short-toed treecreeper, 26 for song thrush and 74 for winter wren.

For many species, we found differences in FID between heavily frequented and the less frequented forest (figure 1 and tables 1, 2). Overall, birds in the less frequented forest showed larger FIDs compared to heavily frequented forests although the strength of this difference was species dependent (see figure 1, table 2). Within species FIDs between the two heavily frequented forests never differed substantially between each other (see table 2).

The higher above ground a bird was located, the shorter was its FID (table 1), whereas the starting distance was positively correlated with the FID (table 1).

DISCUSSION

We found that birds had shorter FIDs in the frequently visited forests than in the less frequented forest. This indicates that the shorter FID is due to human presence, because the habitat was very similar. It also indicates that the shorter FIDs found in urban than rural environments (Cavalli *et al.* 2016) may be mainly due to human presence rather than habitat differences. People may be perceived by naive wildlife as predators (Frid & Dill 2002; Beale & Monaghan 2004a). This may explain why we find large FIDs in forests where birds did not have that much experience with humans (“non-habituated”). However, in forests with higher human frequentation birds could have “habituated” to non-threatening recreationists and reduce their behavioural anti-predatory response. An alternative possible explanation for our finding could be a redistribution of personalities, as recently shown by Sprau & Dingemanse (Sprau & Dingemanse 2017). That is, they showed that personality types are non-randomly distributed along an urban gradient with bolder animals being more frequent in urban areas and shyer individuals in more sub-urban areas. This might also partially explain why we found for most species shorter FIDs in the heavily frequented forests, compared to the less frequented one, but whether non-random settlement or phenotypic plasticity is the driving factor cannot be disentangled with our data.

In conclusion, FID can be affected by human frequentation. Thus, when FID is to be used for defining set-back distances, local FIDs should be measured to avoid mismatching between bird tolerances in areas where the FID was measured and the ones in the local area where it will be applied. If human disturbance already occurred at a given site, the most vulnerable species or individuals might already have left the site, therefore FIDs always have to be used as minimal set-back distances (although mostly average FID plus one or two standard deviations are used). Our finding implies that future studies,

measuring FIDs, should also incorporate site-specific human recreation intensity as a modulating factor for FIDs.

ACKNOWLEDGMENTS

We thank M. Romanski and R. Schmidt who permitted us to measure FIDs in the Forêt de Chaux and the Sihlwald. The following people measured FIDs and we thank them for their effort: B. Garde, H.F. Lemke, and J. Vasseur.

TABLES

Table 1: Model output of the FID-model with the mean FID estimate and the corresponding 95 % credible interval (CrI). The reference category is the Common blackbird from the Allschwilerwald.

Variable	Mean FID estimate	95% CrI
Intercept	12.43	(6.53; 18.36)
Starting distance	6.94	(6.38; 7.50)
Height	-2.51	(-3.06; -1.97)
Time	-0.23	(-0.72; 0.26)
Julian date	-0.09	(-0.58; 0.40)
Forêt de Chaux (FdC)	13.69	(8.62; 18.60)
Sihlwald (Sw)	-2.99	(-6.72; 0.77)
Common chaffinch (CC)	-3.10	(-10.13; 4.12)
Short-toed treecreeper (StT)	-8.17	(-16.56; 0.24)
Eurasian nuthatch (EN)	-4.48	(-11.65; 2.81)
Great tit (GT)	-2.42	(-9.44; 4.68)
European robin (ER)	-4.14	(-11.32; 3.10)
Song thrush (ST)	-7.15	(-13.66; -0.60)
Marsh tit (MT)	-2.58	(-10.17; 5.22)
Winter wren (WW)	-4.03	(-11.32; 3.05)
Forest (FdC) × Species (CC)	-7.00	(-12.44; -1.41)
Forest (FdC) × Species (StT)	-7.49	(-15.22; 0.18)
Forest (FdC) × Species (EN)	-10.37	(-16.10; -4.50)
Forest (FdC) × Species (GT)	-12.37	(-17.66; -7.00)
Forest (FdC) × Species (ER)	-7.74	(-13.34; -2.16)
Forest (FdC) × Species (ST)	-7.36	(-15.68; 1.15)
Forest (FdC) × Species (MT)	-13.01	(-19.61; -6.48)
Forest (FdC) × Species (WW)	-11.02	(-16.81; -5.13)
Forest (Sw) × Species (CC)	3.27	(-1.38; 7.95)
Forest (Sw) × Species (StT)	4.89	(-3.10; 12.67)
Forest (Sw) × Species (EN)	3.57	(-2.47; 9.53)
Forest (Sw) × Species (GT)	2.34	(-2.79; 7.50)
Forest (Sw) × Species (ER)	2.88	(-2.01; 7.71)
Forest (Sw) × Species (ST)	7.76	(0.14; 15.40)
Forest (Sw) × Species (MT)	4.48	(-2.16; 10.98)
Forest (Sw) × Species (WW)	3.46	(-1.58; 8.38)

Table 2: Within species posterior probabilities between forests. Posterior probabilities can take values between 0.5 (no difference) and 1 (fully different) and are a measure to represent the strength of a difference between two measures (levels). The “Forêt de Chaux” (FdC) was seldom used for recreation whereas the other two forests (Allschwilerwald: Aw and Sihlwald: Sw) were heavily frequented by recreationists.

Species	Aw vs FdC	Sw vs FdC	Aw vs Sw
Common blackbird	>0.99	>0.99	0.94
Common chaffinch	>0.99	>0.99	0.59
Short-toed treecreeper	0.98	0.91	0.70
Eurasian nuthatch	0.98	0.88	0.59
Great tit	0.87	0.87	0.64
European robin	>0.99	>0.99	0.52
Song thrush	0.97	0.72	0.92
Marsh tit	0.62	0.63	0.71
Winter wren	0.95	0.90	0.61

FIGURES

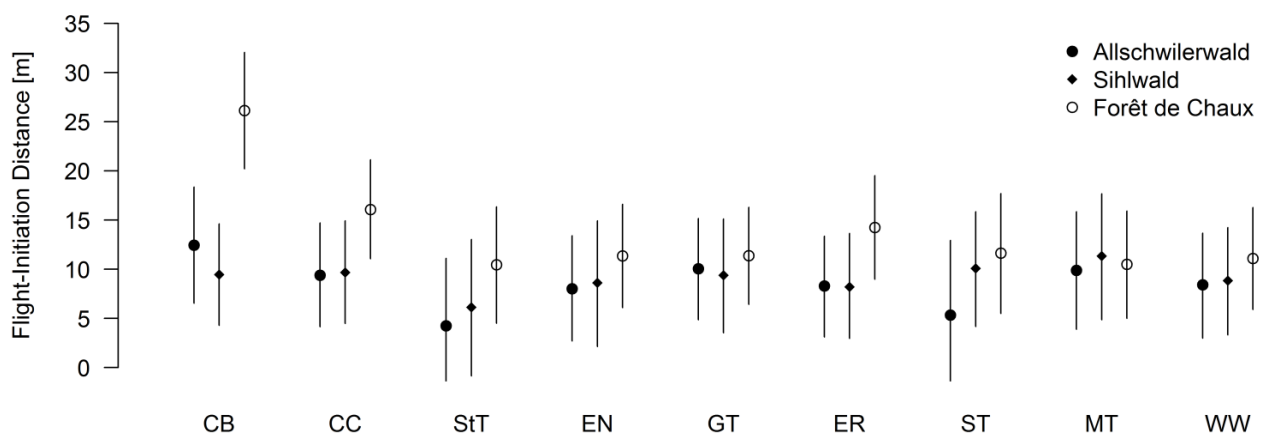


Figure 1: Model estimates (\pm 95 CrI) of species-specific flight-initiation distances for the three different study sites. The “Forêt de Chaux” is rarely frequented by humans (open symbol) whereas the two other forests (closed symbols) are highly frequented by humans. Explanation of the acronyms: CB: Common blackbird (*Turdus merula*), CC: Common chaffinch (*Fringilla coelebs*), StT: Short-toed treecreeper (*Certhia brachydactyla*), EN: Eurasian nuthatch (*Sitta europaea*), GT: Great tit (*Parus major*), ER: European robin (*Erithacus rubecula*), ST: Song thrush (*Turdus philomelos*), MT: Marsh tit (*Poecile palustris*), WW: Winter wren (*Troglodytes troglodytes*).

CHAPTER 3

Experimental evidence of human recreational disturbance effects on bird-territory establishment

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Illustration credit: Fanny le Bagousse (Former trainee)

Experimental evidence of human recreational disturbance effects on bird-territory establishment

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ABSTRACT

The worldwide increase in human outdoor activities raises concerns for wildlife. Human disturbances, even at low levels, are likely to impact species during sensitive periods of the annual cycle. However, experimental studies during the putative sensitive period of territory establishment of birds which not only investigate low disturbance levels, but which also exclude the effect of habitat modification (e.g. walking trails) are lacking. Here, we experimentally disturbed birds in forest plots by walking through twice a day during territory establishment. Later we compared the breeding bird community of experimentally disturbed plots with that of undisturbed control plots. We discovered that the number of territories (-15.0%) and species richness (-15.2%) in disturbed plots were substantially reduced compared to control plots. Species most affected included those sensitive to human presence (assessed by flight-initiation distances), open-cup nesters and above-ground foragers. Long-distance migrants, however, were unaffected due to their arrival after experimental disturbance took place. These findings highlight how territory establishment is a sensitive period for birds, when even low levels of human recreation may be perceived as threatening, and alter settlement decisions. This can have

important implications for the conservation of species, which might go unnoticed when focussing only on already established birds.

Key words: Forest birds, nesting guild, foraging guild, flight-initiation distance, nature-based activities, outdoor recreation.

INTRODUCTION

Outdoor recreational activities have increased substantially in the past decades (Boyle & Samson 1985; Balmford *et al.* 2009), which has led to repeated encounters between people and wildlife. These encounters may provoke wildlife responses, such as increased vigilance, heightened stress-hormone levels, anti-predator escape responses and, in some cases, a decrease in survival and/or reproduction or even abandonment of an area (Ikuta & Blumstein 2003; Thiel *et al.* 2008; Mathot *et al.* 2012; Arlettaz *et al.* 2015; Tarjuelo *et al.* 2015; Tablado & Jenni 2017). Wildlife responses to human recreation will not only depend on the characteristics of the animals involved (e.g. species, sex) and on the type of human disturbance (e.g. noise level, number of people), but also on the environmental conditions (e.g. habitat) and on the specific period in an animal's life history in which the encounter with humans occurs (Tablado & Jenni 2017).

The timing of disturbance events also warrants more attention from researchers (Buckley 2013). Although a number of studies have been conducted during sensitive periods, such as reproduction or other periods of energetic constraints (Arroyo & Razin 2006; Strasser & Heath 2013; Arlettaz *et al.* 2015; Martín *et al.* 2015), territory establishment remains understudied (Götmark 1992; Tablado & Jenni 2017). During this phase, even low-intensity and short-lasting disturbance events could prompt animals to perceive habitats as risky and influence their decision on where to breed, thus altering the density and species richness of the breeding community. An increase from no disturbance to low-level disturbance is likely to have a proportionally stronger ecological impact than a change from low to medium-level disturbance, or from medium to high-level disturbance (Hill *et al.* 1997; Steidl & Powell 2006; Steven, Pickering & Castley 2011; Monz, Pickering & Hadwen 2013). This may apply particularly to the sensitive phase of territory establishment.

In the field of avian biology, human outdoor recreation has been linked to lower abundance and reduced species richness (Van der Zande *et al.* 1984; Patthey *et al.* 2008;

Kangas *et al.* 2010). However, these studies did not focus on the underlying processes being altered by disturbance (e.g. prevention from settling vs. later breeding failure), and often cannot separate direct effects of human presence from indirect effects (e.g. habitat alterations normally associated with recreation). That is, human recreational activities are mostly bound to roads or trails and, thus always occur with habitat alterations (Forman & Alexander 1998), which are known to impact species distribution and abundance (Fernández-Juricic 2000; Butler *et al.* 2012). Therefore, experimental studies are needed to determine the direct effects of human presence on birds and the processes involved (Hill *et al.* 1997; Gill 2007).

The aim of this study was to experimentally investigate whether human recreational activities at relatively low levels altered bird-settlement decisions during territory establishment, and thus, the resulting breeding-bird community. We expected that experimental disturbance during territory establishment would lead to lower densities of breeding birds. Depending on species-specific tolerances towards disturbance, we also predicted changes in species richness and composition. Notably, we expected a reduction in the abundance and number of bird species sensitive to human disturbance, such as ground-nesting, ground-foraging (Langston *et al.* 2007; Mallord *et al.* 2007; Kangas *et al.* 2010; Thompson 2015), and disturbance-sensitive species (Blumstein *et al.* 2003; Weston *et al.* 2012; Livezey, Fernández-Juricic & Blumstein 2016).

MATERIALS AND METHODS

Study site

This study was done in the “Forêt domaniale de Chaux”, a large (200 km²) oak-hornbeam forest in eastern France (47°05'N, 05°40'E) fulfilling all legal and animal welfare regulations (permit number 2014157-0012 of the “Direction Régionale de l'Environnement, de l'Aménagement et du Logement de Franche-Comté”). This forest is subdivided into approximately rectangular 10 ha plots, where harvest is managed by the “Office Nationale des Forêts”. The plots were separated from each other by small treeless tracks but otherwise natural vegetation, generated by harvest-machines. One side was bordered by a gravel road. The forest was only accessible to the public on foot or by bike, with the exception of two paved roads crossing the forest. Recreational activities were concentrated mainly near the town of Dole (23,000 inhabitants) located at the western border of the forest (figure 1) and near Besançon (117,000 inhabitants) which is 15 km to the east of the forest. In most of the forest, the frequency of human recreational activities was extremely low, and occurred primarily in autumn (i.e. mushroom collection and hunting). During our fieldwork (continuous from March to June of 2014 and 2015, 50 h / week) we rarely saw people off-trail within the plots (less than one person per month) and approximately one person per week on the gravel roads near the study plots.

Experimental design

We used plots (mean size: 9.2 ha, range: 7.5 - 13 ha) in the centre of the forest (> 9 km from Dole and Besançon, figure 1) where no timber harvesting occurred during the study period (2014-2015; as agreed with the “Office National des Forêts”). The composition and structure of the vegetation was homogeneous within plots and similar among plots. The plots were dominated by pedunculate oaks *Quercus robur*, many older than 100 years (M. Romanski pers. comm.), with admixed European beech *Fagus*

sylvatica and European hornbeam *Carpinus betulus*, as well as Norway spruce *Picea abies* or Douglas fir *Pseudotsuga menziesii* in small numbers. The plots were at least 600 m apart from each other to prevent confounding neighbouring effects. We divided all plots in two halves (split-plots, mean 4.7 ha); one half was experimentally disturbed while the other half served as a control. The split-plots receiving the disturbance treatment were chosen randomly with the only constraint that half of them were bordered by the gravel road and the other half not.

Since our objective was to examine the effect of human recreation during bird-territory establishment, we only disturbed birds during the pre-breeding season, from early March until mid-April (7 March - 22 April) (von Blotzheim, Bauer & Bezzel 1993). Disturbance events consisted of a group of two or three people, carrying a loudspeaker (Hama, smartphone speaker, power: 3 W with a Samsung digital audio player F3) and walking through a pre-established mower-pattern transect with back and forth lines separated by 20 m (figure 1). The loudspeakers were continuously playing human conversations (obtained from several sources and languages; from TV shows to audio books) at an average human-conversation volume level (approximately 60 dB at 1 m distance (Byrne *et al.* 1994; Hacki 1996)). The orientation of the path was turned 90 degrees from one disturbance event to the next to reduce predictability of the disturbance. These disturbance events lasted around 45 minutes depending on the split-plot area (mean = 42 min, sd = 13 min) and occurred one to three times per day during daytime. The order in which the split-plots were disturbed changed daily to avoid biases in the time of disturbance.

Due to logistic reasons and man-power limitations, the experimental disturbance in 2014 was restricted to six treatment plots which were disturbed on average 1.6 times per day (each plot at least once each day). In 2015, we were able to extend the experiment to 12 plots which were disturbed 2.3 times per day (each plot at least once per day). In the

case of the six plots that were common for both years, we switched the disturbed and control split-plots from one year to the next to exclude possible split-plot-specific effects. In 2014, we therefore disturbed each of the six split-plots 73 times during 45 days, and in 2015, each of the 12 split-plots 105 times during 46 days. The low number of disturbance events allowed us to examine the effects of recreation at intensities much lower than most previous studies in recreation ecology (see for example (Van der Zande *et al.* 1984; Beale & Monaghan 2004a)), thus enabling us to test whether even low levels of disturbance could have an impact when applied during sensitive periods.

Bird territory mapping

The breeding bird territories were censused in all plots three times per season in both years of the study (first census round 20 April – 6 May, second 6 May – 22 May, third 28 May – 17 June) to include the breeding season of all forest-bird species, from residents to late-arriving long-distance migrants. We did not census earlier, to be sure that birds were already settled and that we did not disturb the control split-plots during the territory establishment period. Censuses started at sunrise and lasted 30 to 66 minutes (mean = 42 min) depending on plot size. Censuses followed the Swiss standard breeding-bird survey protocol (Bibby *et al.* 2000; Schmid & Spiess 2008) and consisted of recording all birds seen or heard showing territorial behaviour on a map, while following a mower-pattern transect (lines 60 m apart) covering the entire plot (including both disturbed and control split-plots; figure 1). The censuses were performed by the same two observers in both years, each of which always surveyed the same plots. For each round, we determined the number of contacts per species, but counted pairs and families as one to approach the *number of territories* detected. Long-distance migrants were not considered as breeders, but as transients, if seen or heard before usual arrival dates (according to Schmid *et al.* (Schmid *et al.* 1998); see electronic supplementary material table S1).

Vegetation surveys

In June 2015, we characterised the vegetation of all twelve plots by using a stratified random sampling, i.e. distributing one survey point per 0.5 ha grid cell, which resulted in 7 to 13 points per split-plot (210 survey points in total, figure 1). At each point the following variables were measured: canopy cover (visual estimation of percentage of cover in the observer's visual field when looking straight up; always measured by the same person), ground vegetation cover (in 2x2 m quadrats), shrub cover (in 3x3 m quadrats), and number of trees per species and standing dead trunks with diameter at breast height (dbh) larger than 5 cm in 8x8 m quadrats. Before analyses, we averaged vegetation measures to create mean values per split-plot. There were no significant within-plot differences in any of the vegetation variables between the disturbed and the control split-plots (pairwise t-tests or Wilcoxon tests, depending on data distributions, $p > 0.05$).

Data analysis

We tested for the effect of human disturbance during territory establishment on the number of territories and on species richness, both following a Poisson distribution, with two separate generalized linear mixed models (GLMM) (table 1). The factor *disturbance* treatment (disturbed vs. control split-plot) was included as explanatory variable. To differentiate between birds whose territory-establishment period overlapped with the experimental treatment (residents and short-distance migrants) and long-distance migrants arriving afterwards and not being exposed to the disturbance, both number of territories and species richness were calculated separately for these two groups and a two-level factor *migration type* ("long-distance migrants" vs. "others"; see electronic supplementary material table S1) was added to the models. To describe the structure and composition of the vegetation we included the following explanatory variables: *ground vegetation cover*, *shrub cover*, *canopy cover*, amount of *deadwood*, and *tree diversity*

(Shannon-diversity index (Spellerberg & Fedor 2003) of the main tree species: pedunculate oak *Quercus robur*, European beech *Fagus sylvatica*, European hornbeam *Carpinus betulus* and two species of conifers; *Picea abies*, *Pseudotsuga menziesii*). Additionally, we incorporated the presence/absence of a gravel road along the split-plot to control for further possible habitat differences between split-plots, the linear and quadratic effect of *Julian date* to account for bird-breeding phenology, and the *year* (2014 vs. 2015) to control for inter-annual differences in the intensity of disturbance and in climatic conditions. We also added the two and three-way interactions between *year*, *disturbance* and *migration type*. We included the *split-plot area* (in ha) into the models to account for unequal plot sizes (Connor & McCoy 1979; Korner-Nievergelt *et al.* 2015). For the model on the number of territories we had to include the logarithm of the split-plot area as an offset term to model territory densities (after Korner-Nievergelt *et al.* (Korner-Nievergelt *et al.* 2015)), while for the model on species richness, we included the quadratic effect of area (*Split-plot area*²).

Additionally, in order to investigate the effects of experimental disturbance on the density and richness of specific types of birds, we classified all bird species according to their *nesting guild* (ground, open-cup, and cavity nesters (Perrins & Cramp 1998)), their tolerance to human approach (*sensitivity*; high vs. low), and their *foraging guild* (ground vs. above ground (Perrins & Cramp 1998)) (see electronic supplementary material table S1). For each of the three classifications, we then applied two models (i.e. for number of territories and species) similar to the ones above, but replacing the factor *migration type* by the factor corresponding to each classification (i.e. *nesting guild*, *sensitivity*, or *foraging guild*). These six models were performed without long-distance migrants (i.e. with only those species whose territory-establishment period overlapped with experimental disturbance). Bird *sensitivity* classes were approximated by using the mean flight initiation distance (FID) of the given species during the breeding period in non-urban areas, as

obtained from Díaz *et al.* (Díaz *et al.* 2013). Low sensitivity species had an average FID lower or equal to the overall median value of FID for all species observed breeding in our plots (median FID = 13.13m), whereas high sensitivity species had FID larger than the overall median FID. We acknowledge that FID might not always truly represent species sensitivity, as modulating factors (e.g. vegetation) may influence birds antipredator behaviour (Tablado & Jenni 2017); however, FID is an acceptable and widely available measure for approximating sensitivity towards human disturbance (Blumstein *et al.* 2003).

In all models, to account for observer effect we included *observer* (two-level factor) as a random factor. To account for variations among rounds and plots, census *round* (first, second, third) and *split-plot-ID* were nested within *plot-ID*. All analyses were performed in R 3.3.0 (R Core Team 2016) with the function *glmer* from package *lme4* (Bates *et al.* 2015). All numeric explanatory variables were standardized (mean = 0 and sd = 1) to facilitate model convergence. We used a Bayesian framework to calculate the 95% credible intervals (Crl) of the parameter estimates and model predictions. To do so we simulated random samples (N = 10,000) from the joint posterior distribution of the model parameters using the function *sim* from the R-package *arm* (Gelman & Su 2015) (electronic supplementary material figure S3 and S4), from which we used the 2.5% and 97.5% quantiles as the lower and upper limit of the 95% Crl. To assess how split-plot type (disturbed and control) interacted with year and bird characteristics, we calculated the posterior probability (between 0.5 and 1; using Monte Carlo simulation) of the hypothesis that the mean number of territories or of species at disturbed sites was lower than at control sites (see figure 2 and 3). Using this approach, higher probabilities represent a stronger difference between treatments. Goodness-of-fit was assessed through visual examination of plotted residuals, and we confirmed that there was no overdispersion (Values of the R-function *dispersion_glmer* always below 1, after Korner-Nievergelt *et al.*, 2015). Note that the numbers of territories and species obtained are not absolute

numbers, since we did not account for imperfect detection. Accounting for imperfect detection would have added a layer of complexity to our models which would have been incompatible with sample size (over-parameterisation) and caused problems of convergence.

RESULTS

Both the number of territories and species richness were substantially lower in disturbed split-plots than in the control ones (table 1, figure 2). Moreover, this effect was only observed for resident and short-distance migrant species which experienced the experimental disturbance (figure 2a,c). It was not observed for species arriving later in the season (long-distance migrants; figure 2b,d). We found a reduction of about 15% in the number of territories for residents and short-distance migrants per mean disturbed split-plot compared to the control split-plot over both years (19.8% in 2014 and 10.2% in 2015). Species richness of resident and short-distance migrants also dropped by 15% in the disturbed split-plots compared to control split-plots (19.4% in 2014 and 10.9% in 2015). Independent of the disturbance treatment, the number of territories detected decreased with Julian date.

The response to experimental disturbance varied depending on the characteristics of the species (electronic supplementary material figure S1 and figure S2). The effect of disturbance appeared to be largest on open-cup nesters compared to cavity or ground nesters (figure 3a; electronic supplementary material table S2). High-sensitivity species showed a stronger negative response to disturbance than low-sensitivity species (figure 3b; electronic supplementary material table S3). Finally, above-ground foragers appeared more affected by disturbance than ground foragers (figure 3c; electronic supplementary material table S4). Overall, there seemed to be a stronger effect of disturbance on the number of territories and species richness in the first year (2014) compared to the second year (2015).

DISCUSSION

Our findings confirm our hypothesis that even low levels of disturbance during territory-establishment, with no concomitant habitat alteration, can have a negative effect on both density of breeding birds and species richness. Such an effect was not apparent in long-distance migrants, as they arrived after the end of the experimental disturbance, and thus, were not exposed to it. These findings are in agreement with Steven *et al.* (Steven, Pickering & Castley 2011) and Monz *et al.* (Monz, Pickering & Hadwen 2013) which state, that even low levels of disturbance (as ours) can have significant importance. Contrary to other experimental studies, which also show a negative link between human disturbance and bird density and/or diversity (Riffell, Gutzwiller & Anderson 1996; Gutzwiller & Anderson 1999; Baines & Richardson 2007; Holm & Laursen 2009), we restricted disturbance to the territory-establishment period. Thus, our results suggest that territory establishment may be a sensitive period, in which human disturbances could greatly affect the density and diversity of breeding birds.

During the territory-establishment period birds select breeding sites, and the presence of humans might “invisibly” lower the quality of the habitat (Reed & Merenlender 2008). A possible explanation for the observed effects could be that birds perceive recreationists as predators (Beale & Monaghan 2004a). Indeed, the presence of predators has been shown to strongly affect breeding-site selection (Norrdahl & Korpimäki 1998; Fontaine & Martin 2006). Birds are therefore anticipated to select against habitats with more recreational activity, resulting in altered breeding-bird communities as shown in this study. These results emphasize the important role played by human disturbance on species abundance and diversity.

As predicted, we found that the effect of experimental disturbance varied according to species characteristics. Open-cup nesters were more affected than cavity nesters. This finding is in accordance with Kangas *et al.* (Kangas *et al.* 2010) and Martin & Li (Martin &

Li 1992) suggesting that cavities confer extra protection, which lowers the effect of disturbance and predation. Surprisingly, we did not observe an effect of experimental recreation on ground-nesting birds, as has been previously suggested by Kangas *et al.* (Kangas *et al.* 2010). Similarly, there was no effect of experimental disturbance on ground-foragers. This was probably due to the low number of ground-nesting and ground-foraging species in our study sites (see electronic supplementary material table S1), making an effect of disturbance hard to detect. As expected, we demonstrated a stronger impact of experimental disturbance on the more sensitive species (i.e. with larger flight initiation distance (FID)) than on the less sensitive species. Species with larger FID are generally larger-bodied species (Blumstein *et al.* 2005) and therefore human disturbance is expected to affect these species the most.

The negative response of birds to the experimental disturbance in the first study year was stronger than in the second year, despite increased disturbance intensity in the second year. This finding could be a consequence of the greater total number of territories found in the second year, which could have forced birds to also accept non-preferred (i.e. disturbed) habitats (Komdeur *et al.* 1995; Reijnen *et al.* 1995; Ferrer & Donazar 1996; Rodenhouse *et al.* 2003), diminishing the differences between treatments in the second study year. Habituation effects, on the other hand, can be ruled out due to the treatment switching from the first to the second study year. Carry-over effects from the first to the second year in interaction with treatment switching, could also partially explain this inter-annual difference in impact. That is, if birds experiencing the disturbance split-plot in the first year tried to avoid it in the second year, this could lead to lower starting numbers in this split-plot which became the control split-plot in the second year. This uneven starting number could have partially obscured the effect of disturbance the second year. However, the overall increased numbers of territories in both split-plots in the second year suggest that these carry-over effects, if at all present, would play only a marginal role. Another

partial explanation to this decreased effect in the second year could be differences in weather conditions or food availability was better in the second year, thus increasing the perceived quality of disturbed split-plots. Unfortunately, we did not measure food resources.

Our findings highlight how the impacts of disturbance can go unnoticed when examined later in the season. Indeed, individuals and species establish breeding territories early in the season. A pre-selection in favour of bolder personalities and species might have already occurred during the pre-breeding phase of territory establishment (by tourists or researchers visiting and area). We should therefore be careful when planning and interpreting the results of studies occurring during the breeding season *sensu stricto*. Future studies should investigate the consequences of these recreation-driven reductions in number of territories and species for subsequent breeding parameters, survival, and overall population dynamics.

In conclusion, this study emphasizes that negative effects of human recreational disturbance can already occur after low-intensity disturbance events, even when occurring over a short time period. This is especially relevant during territory establishment in early spring, when improving weather conditions entail an increase in outdoor recreation (at least in temperate regions; R. Schmidt unpublished data). Given the potential conservation implications of these results, we suggest that conservationists and park managers should not only manage disturbance during the main breeding season, but also during territory establishment. Disturbance management could include limiting human access to certain areas that are likely to be used by vulnerable species to establish breeding territories. Additionally, the network of trails open to the public could be reduced temporarily to increase the size of the undisturbed patches. Furthermore, appropriate information should be provided to visitors about the importance of staying on trails to minimize their impacts on wildlife. These measures could help protect sensitive birds (species or individuals of

certain personalities) that would settle in an area if there were no human activities during the pre-breeding season.

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TABLES

Table 1: Results of the GLMMs testing the effect of experimental disturbance (human recreation) on the number of bird territories and species richness. Represented are the estimates of the effect of each variable with the corresponding 95% credible intervals (Crl).

Terms	Number of Territories		Species richness	
	Estimate	Crl	Estimate	Crl
Intercept	0.8810	0.5780; 1.1814	1.9444	1.6828; 2.2046
Disturbance				
disturbed	-0.2232	-0.4308; -0.0092	-0.2151	-0.4790; 0.0584
control	/	/	/	/
Type				
others	/	/	/	/
long-distance migrant	-3.9117	-4.8799; -2.9224	-3.4014	-4.3907; -2.3873
Ground vegetation cover	0.0253	-0.0723; 0.1203	-0.0261	-0.1163; 0.0664
Shrub cover	0.1084	-0.0125; 0.2260	0.1057	-0.0151; 0.2272
Canopy cover	0.0294	-0.0855; 0.1478	-0.0343	-0.1736; 0.1071
Tree diversity	-0.0235	-0.1224; 0.0738	-0.0728	-0.1704; 0.0261
Deadwood	0.0259	-0.0806; 0.1336	0.0479	-0.0782; 0.1735
Road				
presence	0.0190	-0.1559; 0.1941	-0.0226	-0.2317; 0.1800
absence	/	/	/	/
Juliandate	-0.1231	-0.2153; -0.0328	-0.0155	-0.1327; 0.1072
Juliandate ²	-0.0524	-0.1555; 0.0529	-0.0111	-0.1405; 0.1184
Year				
2014	/	/	/	/
2015	0.1018	-0.0801; 0.2828	0.0519	-0.1757; 0.2807
Surface	-0.0502	-0.1469; 0.0461	0.2374	-0.7693; 1.2876
Surface ²	-	-	0.9647	-0.1803; 2.0994
Disturbance × Type				
disturbed: long-distance migrant	-0.0873	-1.5989; 1.3863	-0.1135	-1.6684; 1.3940
Disturbance × Year				
disturbed: 2015	0.1131	-0.1484; 0.3746	0.0966	-0.2403; 0.4227
Type × Year				
long-distance migrant: 2015	0.3329	-0.8118; 1.4819	0.3098	-0.8357; 1.4698
Disturbance × Type × Year				
disturbed: long-distance migrant: 2015	0.2277	-1.4639; 1.9970	0.2847	-1.4482; 1.9820

/ = reference categories

- = Parameter not tested in the given model

Distribution = Poisson; link function = natural logarithm; random factors = observer, round and split-plot ID nested within plot ID.

FIGURES

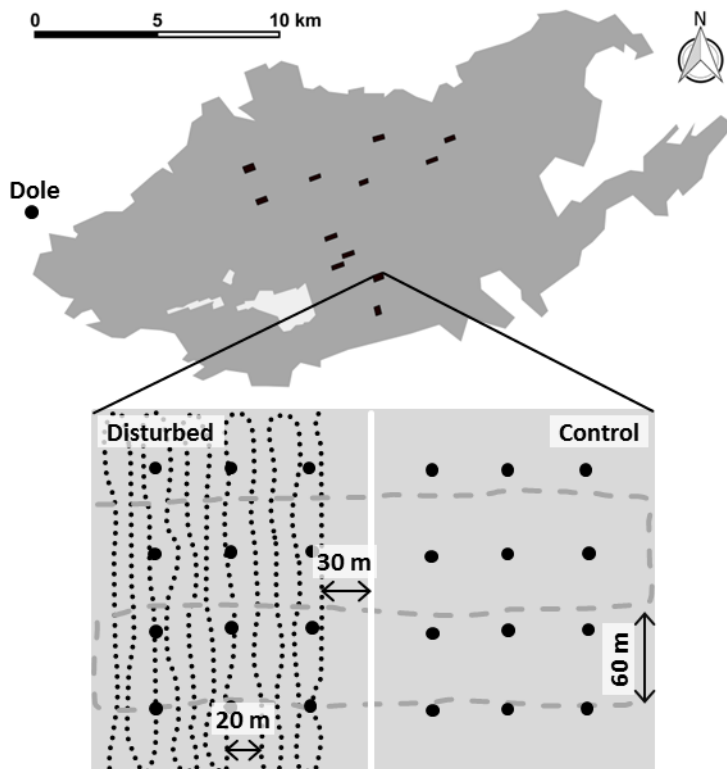


Figure 1. Study site “Forêt domaniale de Chaux” (dark grey area) with the twelve different plots (black rectangles) and “Dole” as the next town. Shown in detail is a schematic representation of a study plot with the two split-plots (one disturbed, one control). The black-dotted line represents an example of a disturbance walk (the orientation of this transect was turned 90° between disturbance events). A 30 m buffer was left between the disturbance path and the line separating the split-plots (white-continuous line), to lower a potential confounding effect into the control split-plot. This distance was selected considering the information available in the literature about flight initiation distances (FID) of bird species found in this forest (FID for more than 80% of the species is below 30 m). The grey-dashed line represents the breeding-bird census transect and the individual black dots are vegetation-survey points (for simplicity depicted systematically, although stratified random sampling was used).

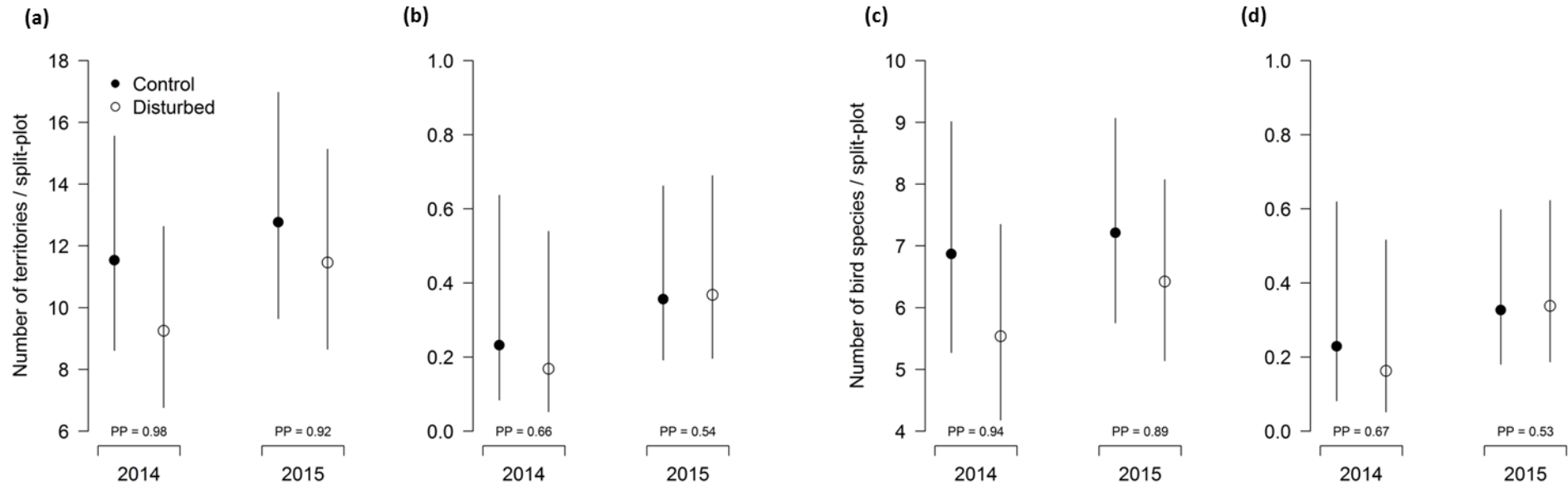


Figure 2. Effects of experimental human disturbance on the number of territories (*a, b*) and species richness (*c, d*) per split-plot (4.7 ha) according to *year* and *migration type*: the graphs (*a*) and (*c*) include only the resident and short-distance migrant species, while the graphs (*b*) and (*d*) only the long-distance migrants. Note the different y-axes. Represented are mean fitted values with 95% credible intervals (table 1) and the posterior probability (PP, from 0.5 to 1) that the difference between disturbed and control split-plots is different from zero. The larger the PP the more likely it is that disturbed and control split-plots are different.

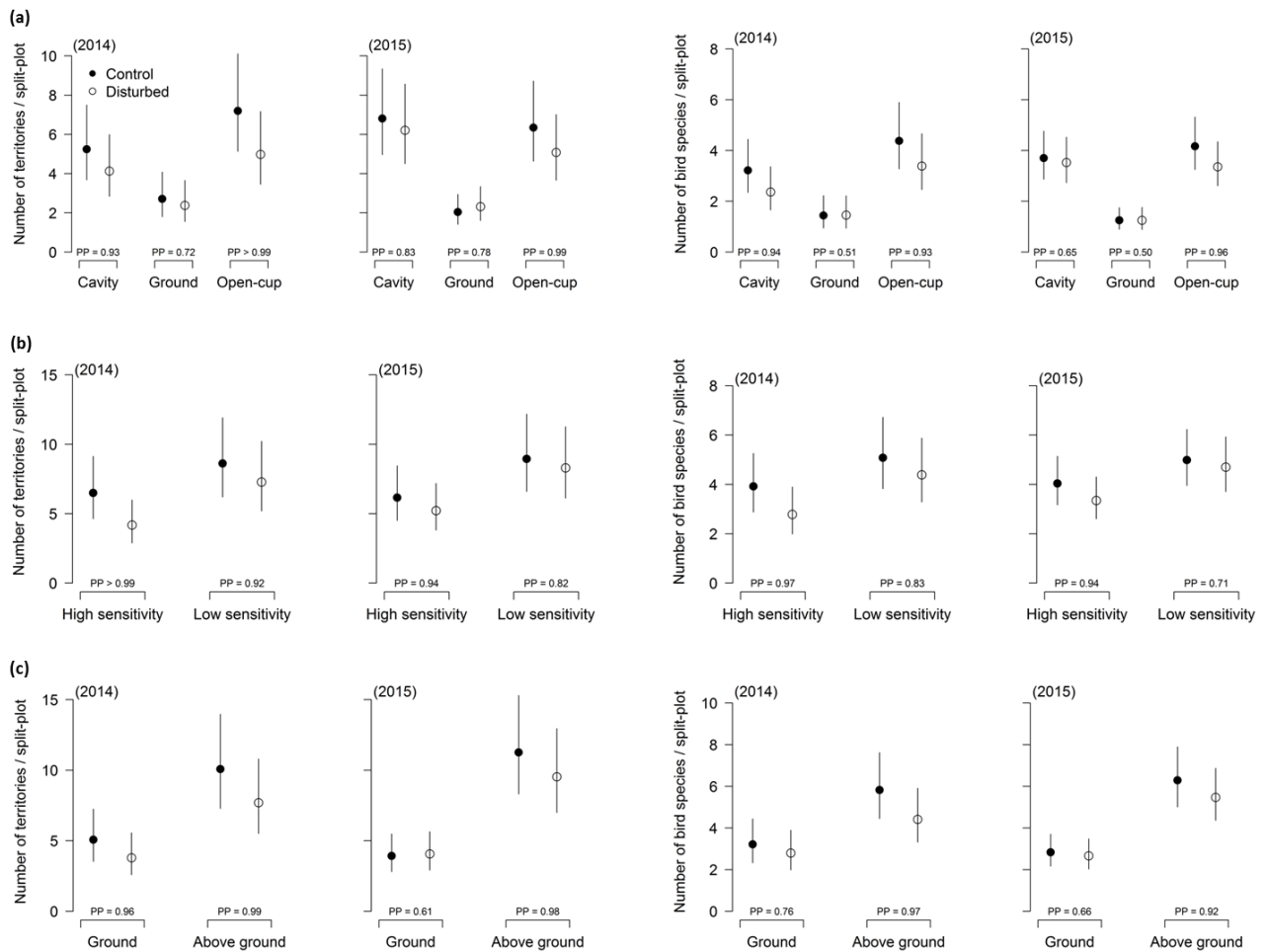


Figure 3. Effect of experimental human disturbance on the number of territories and species richness per split-plot (4.7 ha) according to (a) nesting-guild (cavity, ground and open-cup nesters), (b) sensitivity of the species (high = FID > median FID, low = FID ≤ median FID), and (c) foraging guild (ground and above ground) in 2014 and 2015, respectively (only for residents and short distance migrants). Represented are mean fitted values with 95% credible intervals and the corresponding posterior probabilities (PP) that the differences between disturbed and control split-plots are different from zero.

SUPPORTING INFORMATION

Table S1. Bird species recorded during the breeding bird censuses in 2014 and 2015 (n = 34), with their scientific and English names, as well as the abbreviations used for the figures (Electronic supplementary material figure S1 and S2). We also added the threshold dates after which a species was considered as a breeding bird and not a migrant passing through (according to [37]), and the classification into *migration type* (long-distance migrants versus others (residents and short-distance migrants)), *nesting guild* (cavity, ground and open-cup nesters), *foraging guild* (ground, above ground) and *sensitivity* according to flight initiation distance (FID); FID > median FID = high sensitivity, FID ≤ median FID = low sensitivity.

Scientific name	Abbreviation	English name	Threshold date	Typ ¹	Nesting guild ¹	Foraging guild ¹	Sensitivity ²
<i>Aegithalos caudatus</i>	AEGCAU	Long-tailed Tit	15 April	Others	Open-cup	Above ground	Low
<i>Anthus trivialis</i>	ANTTRI	Tree Pipit	25 April	Long-distance migrant	-	-	-
<i>Buteo buteo</i>	BUTBUT	Common Buzzard	15 April	Others	Open-cup	Above ground	High
<i>Certhia brachydactyla</i>	CERBRA	Short-toed Treecreeper	15 April	Others	Open-cup	Above ground	Low
<i>Coccothraustes coccothraustes</i>	COCCOC	Hawfinch	15 April	Others	Open-cup	Above ground	High
<i>Columba palumbus</i>	COLPAL	Common Wood Pigeon	15 April	Others	Open-cup	Ground	High
<i>Cuculus canorus</i>	CUCCAN	Common Cuckoo	15 April	Others	Open-cup	Above ground	High
<i>Cyanistes caeruleus</i>	CYACAE	Eurasian Blue Tit	15 April	Others	Cavity	Above ground	Low
<i>Dendrocopos major</i>	DENMAJ	Great Spotted Woodpecker	15 April	Others	Cavity	Above ground	High
<i>Dendrocopos medius</i>	DENMED	Middle Spotted Woodpecker	15 April	Others	Cavity	Above ground	na
<i>Dendrocopos minor</i>	DENMIN	Lesser Spotted Woodpecker	15 April	Others	Cavity	Above ground	na
<i>Erithacus rubecula</i>	ERIRUB	European Robin	15 April	Others	Ground	Ground	Low
<i>Fringilla coelebs</i>	FRICOE	Common Chaffinch	15 April	Others	Open-cup	Ground	High
<i>Garrulus glandarius</i>	GARGLA	Eurasian Jay	15 April	Others	Open-cup	Above ground	High
<i>Lophophanes cristatus</i>	LOPCRI	European Crested Tit	15 April	Others	Cavity	Above ground	Low
<i>Oriolus oriolus</i>	ORIORI	Eurasian Golden Oriole	10 May	Long-distance migrant	-	-	-

<i>Parus major</i>	PARMAJ	Great Tit	15 April	Others	Cavity	Above ground	Low
<i>Periparus ater</i>	PERATE	Coal Tit	15 April	Others	Cavity	Above ground	Low
<i>Phylloscopus collybita</i>	PHYCOL	Common Chiffchaff	15 April	Others	Ground	Above ground	Low
<i>Phylloscopus sibilatrix</i>	PHYSIB	Wood Warbler	1 May	Long-distance migrant	-	-	-
<i>Phylloscopus trochilus</i>	PHYTRO	Willow Warbler	25 April	Long-distance migrant	-	-	-
<i>Picus canus</i>	PICCAN	Grey-headed Woodpecker	15 April	Others	Cavity	Ground	High
<i>Poecile palustris</i>	POEPAL	Marsh Tit	15 April	Others	Cavity	Above ground	Low
<i>Regulus ignicapilla</i>	REGIGN	Common Firecrest	15 April	Others	Open-cup	Above ground	Low
<i>Regulus regulus</i>	REGREG	Goldcrest	15 April	Others	Open-cup	Above ground	Low
<i>Sitta europaea</i>	SITEUR	Eurasian Nuthatch	15 April	Others	Cavity	Above ground	High
<i>Streptopelia turtur</i>	STRTUR	European Turtle Dove	15 May	Long-distance migrant	-	-	-
<i>Sturnus vulgaris</i>	STUVUL	Common Starling	15 April	Others	Cavity	Ground	High
<i>Sylvia atricapilla</i>	SYLATR	Eurasian Blackcap	15 April	Others	Open-cup	Above ground	Low
<i>Sylvia borin</i>	SYLBOR	Garden Warbler	10 May	Long-distance migrant	-	-	-
<i>Troglodytes troglodytes</i>	TROTRO	Eurasian Wren	15 April	Others	Open-cup	Ground	Low
<i>Turdus merula</i>	TURMER	Common Blackbird	15 April	Others	Open-cup	Ground	High
<i>Turdus philomelos</i>	TURPHI	Song Trush	15 April	Others	Open-cup	Ground	High
<i>Turdus viscivorus</i>	TURVIS	Mistle Trush	15 April	Others	Open-cup	Ground	High

¹: Bibby et al. 2000; ²: Díaz et al. 2013; na: no data available, -: not included in this analysis

Table S2. Results of the GLMMs testing the effect of experimental disturbance on the number of territories and species richness according to their nesting guild (Long-distance migrants were not included in these analyses, see electronic supplementary material table S1). Represented are the estimates of the effect of each variable with its corresponding 95% credible intervals (CrI).

Terms	Number of territories		Species richness	
	Estimate	CrI	Estimate	CrI
Intercept	0.0483	-0.3087; 0.3986	1.1631	0.8530; 1.4874
Disturbance				
disturbed	-0.2346	-0.5455; 0.0807	-0.3098	-0.7076; 0.0796
control	/	/	/	/
Guild				
cavity	/	/	/	/
ground	-0.6571	-1.0120; -0.3006	-0.8042	-1.2656; -0.3459
open-cup	0.3208	0.0554; 0.5891	0.3053	-0.0292; 0.6480
Ground vegetation	0.0053	-0.0793; 0.0899	-0.0471	-0.1299; 0.0360
Shrub	0.0779	-0.0266; 0.1821	0.0573	-0.0555; 0.1652
Canopy	0.0288	-0.0787; 0.1341	-0.0451	-0.1716; 0.1652
Tree diversity	-0.0213	-0.1071; 0.0660	-0.0732	-0.1602; 0.0135
Deadwood	-0.0031	-0.0978; 0.0932	0.0057	-0.1096; 0.1213
Road				
presence	0.0556	-0.1013; 0.2101	-0.0081	-0.2001; 0.1772
absence	/	/	/	/
Julian date	-0.1178	-0.2009; -0.0369	-0.0326	-0.1363; 0.0759
Julian date ²	0.0118	-0.0826; 0.1046	0.0229	-0.0944; 0.1363
Year				
2014	/	/	/	/
2015	0.2638	0.0094; 0.5105	0.1381	-0.1785; 0.4572
Split-plot area	-0.0043	-0.0853; 0.0783	0.9629	0.0471; 1.8548
Split-plot area ²	-	-	1.0298	0.0228; 2.0199
Disturbance × Year				
disturbed: 2015	0.1387	-0.2203; 0.4998	0.2598	-0.2037; 0.7344
Guild × Year				
ground: 2015	-0.5492	-0.9891; -0.1033	-0.2793	-0.8464; 0.2898
open-cup: 2015	-0.3911	-0.7079; -0.0620	-0.1872	-0.5968; 0.2193
Disturbance × Guild				
disturbed: ground	0.1008	-0.4181; 0.6215	0.3193	-0.3427; 0.9934
disturbed: open-cup	-0.1343	-0.5497; 0.2759	0.0554	-0.4552; 0.5694
Disturbance × Guild × Year				
disturbed: ground: 2015	0.1248	-0.5289; 0.7614	-0.2708	-1.0868; 0.5439
disturbed: open-cup: 2015	0.0080	-0.4928; 0.5046	-0.2207	-0.8364; 0.3924

/ = Reference categories

- = Parameter not tested in this model

Distribution = Poisson; link function = natural logarithm; random factors = observer, round and split-plot ID nested within plot ID

Table S3. Results of the GLMMs testing the effect of the experimental disturbance on the number of territories and species richness according to their sensitivity towards humans according to flight initiation distances (only resident and short-distance migrants were included in these analyses, see electronic supplementary material table S1). Represented are the estimates of the effect of each variable with its corresponding 95% credible intervals (CrI).

Terms	Number of territories		Species richness	
	Estimate	CrI	Estimate	CrI
Intercept	0.2675	-0.0746; 0.6043	1.3662	1.0782; 1.6631
Disturbance				
disturbed	-0.4433	-0.7342; -0.1508	-0.3408	-0.7058; 0.0209
control	/	/	/	/
Sensitivity				
high	/	/	/	/
low	0.2790	0.0353; 0.5234	0.2582	-0.0578; 0.5698
Ground vegetation	0.0046	-0.0799; 0.0872	-0.0459	-0.1264; 0.0364
Shrub	0.0751	-0.0311; 0.1820	0.0539	-0.0547; 0.1647
Canopy	0.0268	-0.0801; 0.1385	-0.0460	-0.1701; 0.0810
Tree diversity	-0.0223	-0.1106; 0.0623	-0.0762	-0.1627; 0.0087
Deadwood	-0.0065	-0.1021; 0.0897	0.0014	-0.1115; 0.1168
Road				
presence	0.0533	-0.1003; 0.2092	-0.0150	-0.1983; 0.1699
absence	/	/	/	/
Julian date	-0.1218	-0.2048; -0.0403	-0.0369	-0.1414; 0.0713
Julian date ²	0.0148	-0.0808; 0.1104	0.0281	-0.0911; 0.1440
Year				
2014	/	/	/	/
2015	-0.0535	-0.2850; 0.1811	0.0338	-0.2541; 0.3176
Split-plot area	-0.0060	-0.0893; 0.0742	0.8990	0.0159; 1.8099
Split-plot area ²	-	-	1.0680	0.0500; 2.0681
Disturbance × Year				
disturbed: 2015	0.2777	-0.0700; 0.6299	0.1470	-0.2918; 0.5915
Sensitivity × Year				
low: 2015	0.0930	-0.2130; 0.3868	-0.0484	-0.4248; 0.3225
Disturbance × Sensitivity				
disturbed: low	0.2752	-0.1038; 0.6549	0.1987	-0.2661; 0.6651
Disturbance × Sensitivity × Year				
disturbed: low: 2015	-0.1892	-0.6374; 0.2749	-0.0634	-0.6258; 0.4978

/ = Reference category

- = Parameter not tested in this model

Distribution = Poisson; link function = natural logarithm; random factors = observer, round and split-plot ID nested within plot ID

Table S4. Results of the GLMMs testing the effect of experimental disturbance on the number of territories and species richness according to their foraging guild (only resident and short-distance migrants were included in these analyses, see electronic supplementary material table S1). Represented are the estimates of the effect of each variable with its corresponding 95% credible intervals (CrI).

Terms	Number of territories		Species richness	
	Estimate	CrI	Estimate	CrI
Intercept	0.0164	-0.3425; 0.3790	1.1662	0.8441; 1.4838
Disturbance				
disturbed	-0.2922	-0.6133; 0.0225	-0.1403	-0.5187; 0.2421
control	/	/	/	/
Foraging guild				
ground	/	/	/	/
above ground	0.6905	0.4285; 0.9422	0.5933	0.2723; 0.9105
Ground vegetation	0.0051	-0.0785; 0.0883	-0.0467	-0.1286; 0.0360
Shrub	0.0772	-0.0290; 0.1829	0.0575	-0.0504; 0.1644
Canopy	0.0288	-0.0823; 0.1347	-0.0452	-0.1707; 0.0816
Tree diversity	-0.0205	-0.1054; 0.0660	-0.0726	-0.1598; 0.0133
Deadwood	-0.0027	-0.0997; 0.0927	0.0056	-0.1100; 0.1207
Road				
presence	0.0552	-0.1005; 0.2127	-0.0093	-0.1977; 0.1792
absence	/	/	/	/
Julian date	-0.1178	-0.1995; -0.0333	-0.0313	-0.1372; 0.0762
Julian date ²	0.0101	-0.0860; 0.1057	0.0220	-0.0929; 0.1379
Year				
2014	/	/	/	/
2015	-0.2529	-0.5274; 0.0191	-0.1262	-0.4515; 0.1987
Split-plot area	-0.0051	-0.0878; 0.0776	0.9686	0.0647; 1.8545
Split-plot area ²	-	-	1.0306	0.0348; 2.0477
Disturbance × Year				
disturbed: 2015	0.3240	-0.0733; 0.7331	0.0770	-0.3888; 0.5528
Foraging guild × Year				
above ground: 2015	0.3637	0.0398; 0.6917	0.2076	-0.1901; 0.5991
Disturbance × Foraging guild				
disturbed: above ground	0.0234	-0.3597; 0.4042	-0.1368	-0.6103; 0.3280
Disturbance × Foraging guild × Year				
disturbed: above ground: 2015	-0.2227	-0.7073; 0.2558	0.0577	-0.5175; 0.6353

/ = Reference category

- = Parameter not tested in this model

Distribution = Poisson; link function = natural logarithm; random factors = observer, round and split-plot ID nested within plot ID

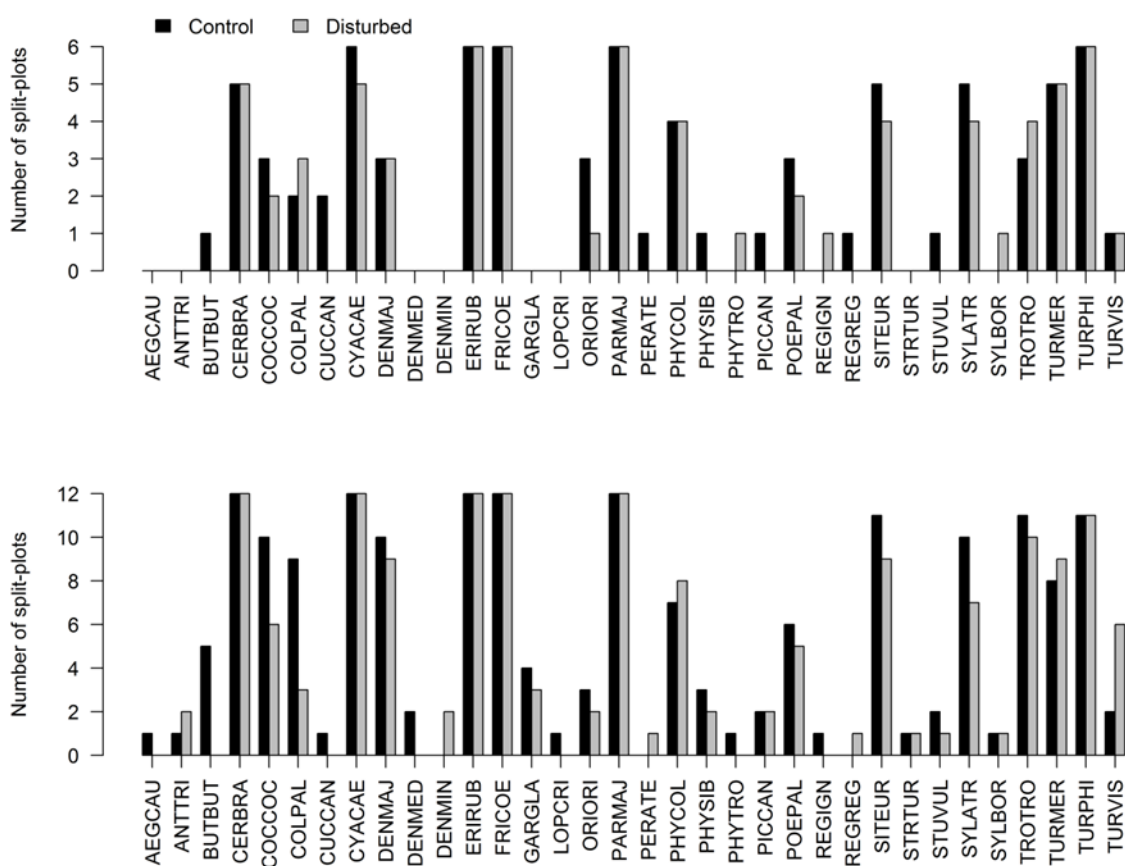


Figure S1. Number of split-plots in which each species was detected at least once during the three breeding-bird censuses, separately for disturbed and control split-plots. In 2014 (a) a species could be seen in a maximum of 6 split-plots while in 2015 (b) the maximum was 12. For species abbreviations see electronic supplementary material table S1.

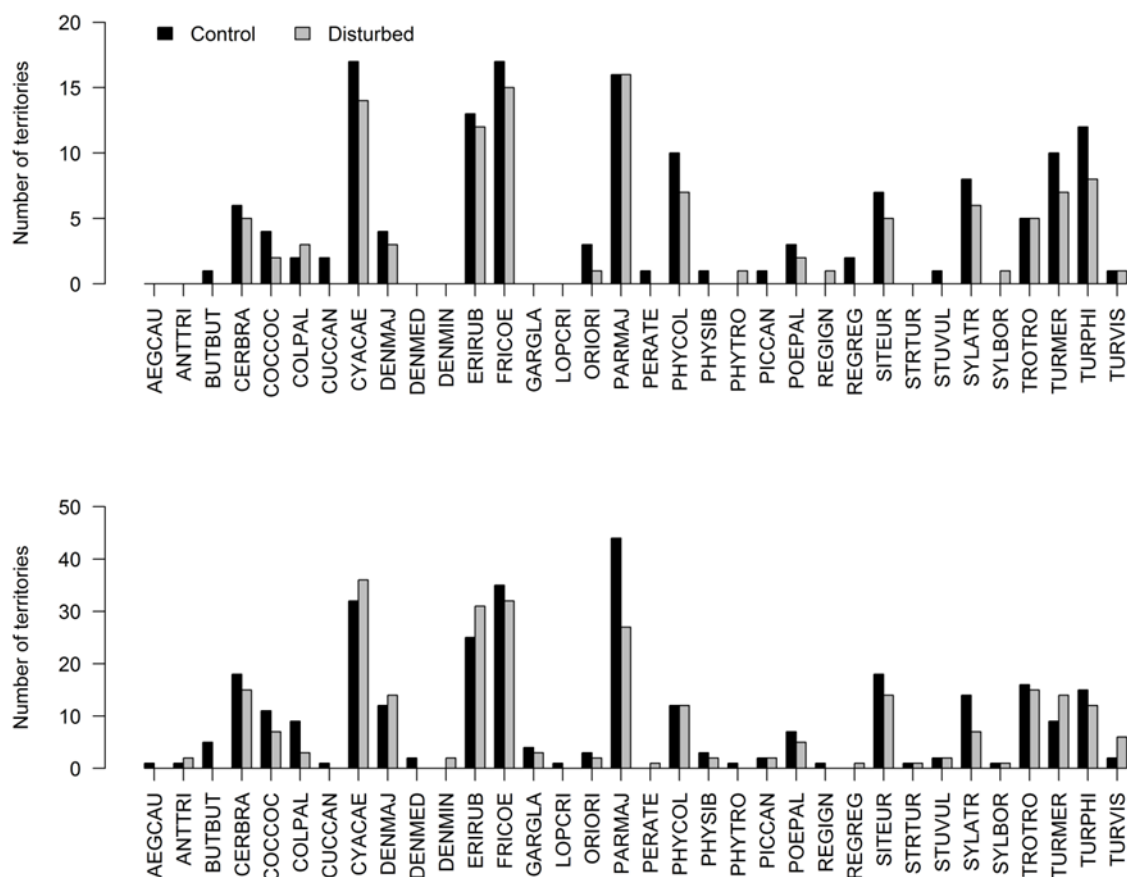


Figure S2. Number of territories per species for disturbed and control split-plots in the six plots of 2014 (a) and in the 12 plots of 2015 (b). For each year, the maximum number of territories per species detected in each split-plot out of the three censuses was taken and summed over all split-plots. For species abbreviations see electronic supplementary material table S1.

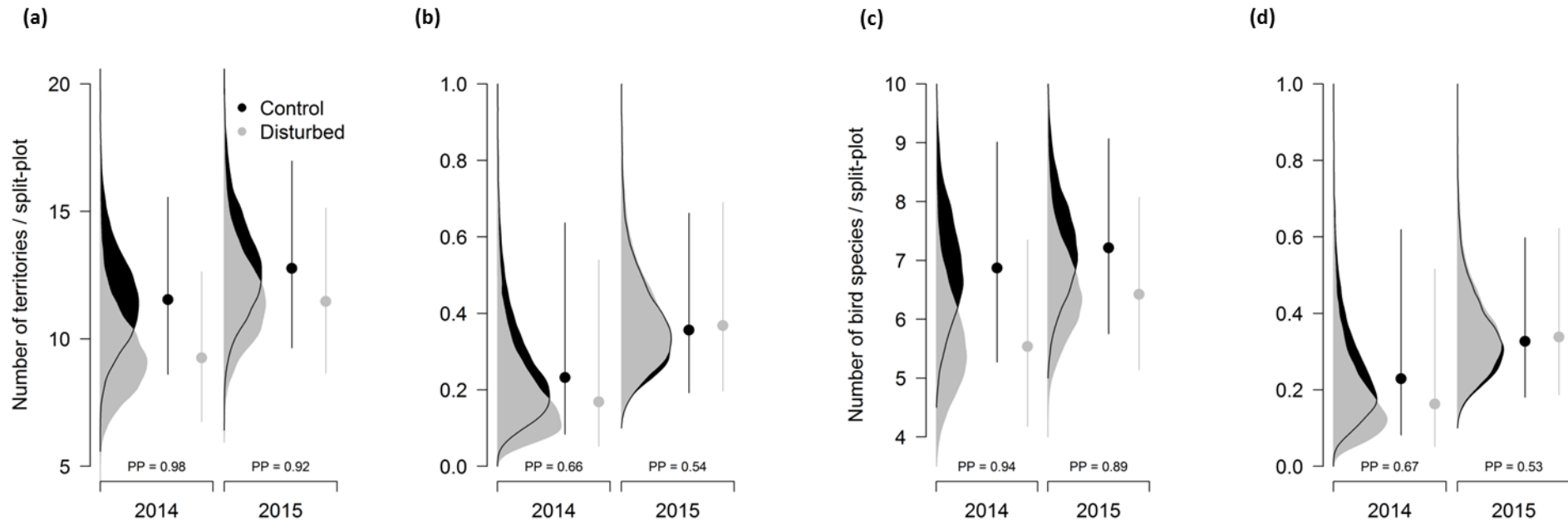


Figure S3. Effect of experimental human disturbance on the number of territories (a,b) and species richness (c,d) per split-plot (4.7 ha) according to *year* and *migration type*: the graphs (a) and (c) include only the resident and short-distance migrant species, while the graphs (b) and (d) only the long-distance migrants. Note the different y-axes. Represented are mean fitted values with 95% credible intervals (table 1) as well as the corresponding posterior distributions. The posterior probability (PP) shows the strength of the difference between disturbed and control split-plots.

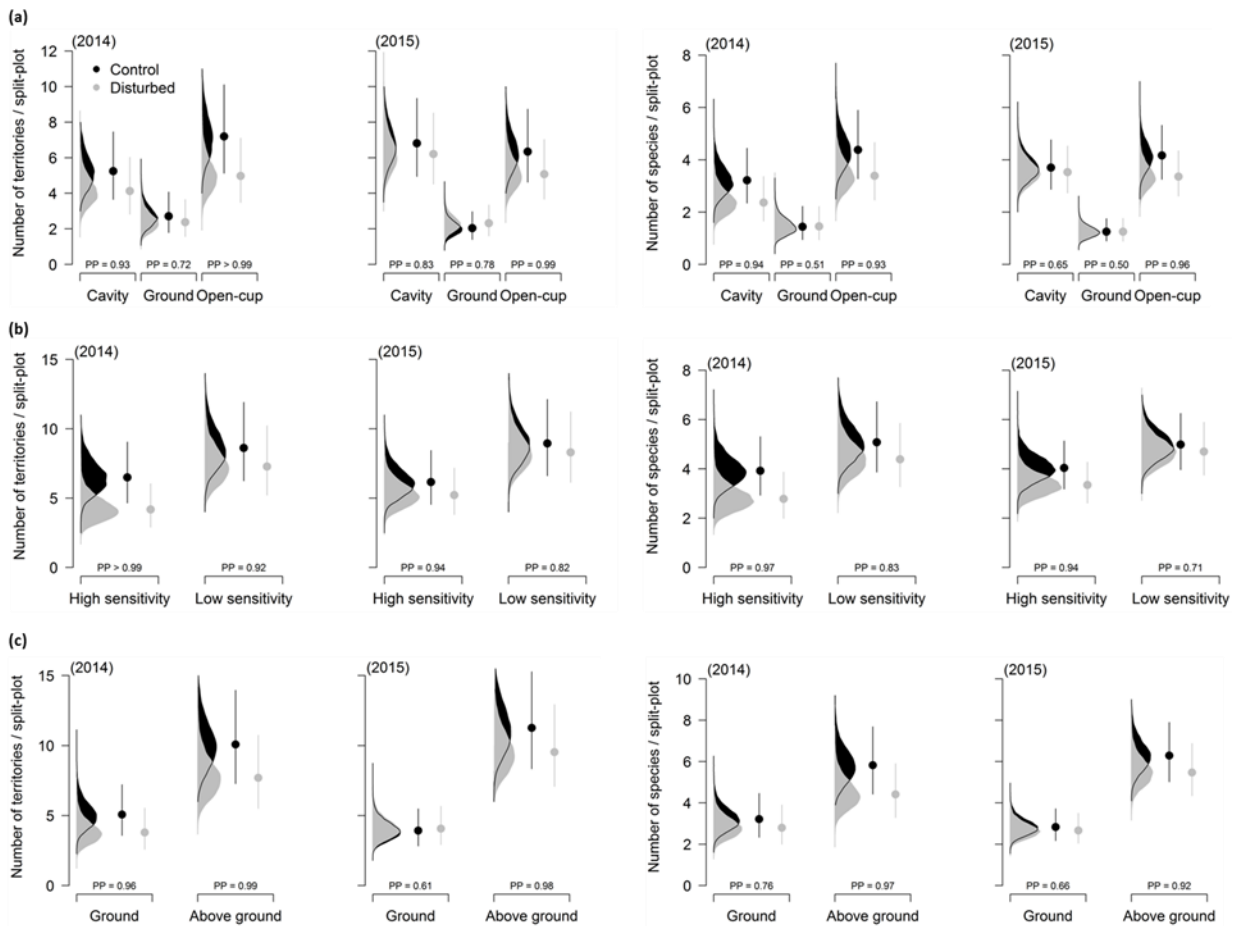


Figure S4. Effect of experimental human disturbance on the number of territories and species richness per split-plot (4.7 ha) according to (a) nesting-guild (cavity, ground and open-cup nesters), (b) sensitivity (based on flight initiation distance (FID); high = FID > median FID, low = FID ≤ median FID), and (c) foraging guild (ground and above ground) in 2014 and 2015, respectively (only for resident and short distance migrants). Represented are mean fitted values with 95% credible intervals (Electronic supplementary material table S2-S4) as well as the corresponding posterior distributions and the posterior probability (PP) that the differences between disturbed and control split-plots are different from zero.

CHAPTER 4

Human recreation decreases maternal antibodies in bird chicks: an overlooked effect of disturbance

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Human recreation decreases maternal antibodies in bird chicks: an overlooked effect of disturbance

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ABSTRACT

Outdoor recreational activities are booming nowadays and animals perceive humans as predators, which trigger behavioural and/or physiological reactions (e.g. heart rate increase, activation of the Hypothalamic-Pituitary-Adrenal axis (HPA)). Hormones have been shown to affect the immune system of a given animal and therefore also the amount of maternal antibodies a female transmits to her offspring. A few studies showed that predator presence affected the amount of maternal antibodies deposited into eggs. We wanted to experimentally test, whether human recreation induces the same predator-like effects in breeding birds, and whether these changes in maternal antibody deposition have an effect on the offspring. Great tit chicks of disturbed mothers had lower maternal antibody titres compared to control chicks. The disturbance impact was depending on the vegetation density, as an interaction between disturbance and shrub cover showed, with denser vegetation reducing the negativ impact of disturbance. The hatching success of great tits was positively correlated with the amount of maternal antibodies deposited. All of the aforementioned findings do not hold for blue tits, but they are apparently mainly affected by the presence of great tits. Chicks which received more maternal antibodies were heavier at an early stage of life, but this positive effect dilutes towards fledging.

Through this dilution of the positive effect of maternal antibodies during chick growth, body mass gain was negatively correlated with maternal antibody titres, but this does not imply a cost of maternal antibodies. We suggest that our findings can be explained through an activation of the HPA-axis, mainly an increase in corticosterone, which is known to have an immunosuppressive action. Therefore human disturbance can negatively affect the survival of chicks at an early life stage, when they are mainly relying on maternal antibodies, and finally this could reduce breeding success and therefore the parents' fitness.

Key words: Outdoor activities, human disturbance, immunology, trans-generational effects, *Parus major*, *Cyanistes caeruleus*

INTRODUCTION

Human sport activities and recreation often occur in nature and may negatively impact wildlife (Larson *et al.* 2016; Bötsch, Tablado & Jenni 2017). Humans are often perceived as predators by wildlife (Frid & Dill 2002), which usually react with behavioural (e.g. flight response; Blumstein, 2010) and/or physiological responses, such as the activation of the hypothalamic-pituitary-adrenal-axis (HPA-axis; Almasi *et al.*, 2015; Fowler, 1999; Thiel *et al.*, 2008). If these behavioural and physiological responses occur frequently they may lead to long term increases in stress levels, which might compromise health and fitness (Tablado & Jenni 2017). For instance, stressed individuals tend to have increased levels of circulating glucocorticoid hormones (Saino *et al.* 2003, 2005; Hayward & Wingfield 2004), which in turn have been shown to have an immunosuppressive function (Råberg *et al.* 1998) and lead to a reduced amount of circulating immunoglobulins (Bourgeon & Raclot 2006; Hargitai *et al.* 2009; Gao, Sanchez & Deviche 2016). These altered levels of glucocorticoids and antibodies can then have trans-generational effects if they are transmitted to the offspring (Rubolini *et al.* 2005; Saino *et al.* 2005). In the case of birds, stressful events occurring during the egg-laying phase may therefore have important impacts on chicks, through stressed mothers depositing higher levels of the main glucocorticoid hormone (i.e. corticosterone in birds) and altered levels of antibodies in the eggs (Saino *et al.* 2005; Hargitai, Prechl & Török 2006; Hargitai *et al.* 2009; Morosinotto *et al.* 2013).

Maternal Antibodies (matAbs) represent the mother's entire repertoire of antibodies against antigens she was exposed to in her life (Lemke, Hansen & Lange 2003; Lemke, Coutinho & Lange 2004) and freshly hatched chicks depend almost entirely on these matAbs for their immune responses up to the first weeks of their life (Grindstaff, Brodie & Ketterson 2003; Pihlaja, Siitari & Alatalo 2006; Gasparini *et al.* 2009). Therefore, the

amount of matAbs deposited into the eggs, positively correlates with chick survival and growth (Pihlaja, Siitari & Alatalo 2006; Grindstaff 2008).

The aim of this study was then to experimentally test, whether human recreational activities during the early breeding season, would trigger anti-predator physiological reactions in breeding females which in turn would result in lower matAb deposition into eggs (measured later in newly hatched chicks). Moreover, we wanted to examine whether this altered deposition of matAbs in eggs was correlated with lower hatching success and chick growth. We predicted that chicks hatched in areas with higher human frequentation would have a lower amount of matAbs compared to broods in control areas with no human frequentation. We also expected that the reduced amount of matAbs would be correlated with reduced hatching success and lower growth rate compared to control chicks.

MATERIALS AND METHODS

Study area and experimental design

The study was carried out in the early breeding season of 2014 and 2015 in the “Forêt domaniale de Chaux” in France (47°05'N, 05°40'E), which is a forest consisting primarily of pedunculate oaks (*Quercus robur*) and European hornbeam (*Carpinus betulus*) and whose harvest is managed by the “Office National des Forêts” (ONF). We worked in 12 plots (mean size 9.2 ha, range: 7.5-13 ha), which fulfilled the following criteria: (1) homogeneous vegetation structure, (2) well separated from each other (> 600 m), to avoid spill-over effects, (3) no timber harvesting in the study plots during the entire study period, and (4) location far away from urban settlements (> 9 km) to reduce other sources of disturbance. In early February 2014 we installed 210 nest boxes (Schwegler, Type B1, with 32 mm entrance diameter) for small cavity nesters (mainly tit species) at a density of about two nest-boxes per ha (i.e. not exceeding the natural breeding density of tits; Krebs, 1971). After the first breeding season, in autumn 2014, we cleaned and removed the nest boxes and installed them again in February 2015, to have twice the same experimental setup for the two study years.

Each plot was divided into two and each split-plot either received an experimental-disturbance treatment (during early spring; 7 March – 22 April in 2014 and 2015, see also Fig. 1) or served as control. The treatment consisted in mimicking a common human recreational activity (i.e. people hiking in the forest), by having groups of 2 to 3 people walking back and forth through the split-plots on a regular mower-pattern transect (distance between walking lines 20 m, for details see Bötsch et al., 2017). This treatment was applied one to three times every day and people were carrying a loudspeaker (Hama, smartphone speaker, power 3W, with a Samsung digital audio player F3) broadcasting human conversation (e.g. TV shows or audio books) at an average volume level of 60 dB at 1 m distance (Byrne *et al.* 1994; Hacki 1996) to reproduce normal hiking conversation.

We varied the direction of the mower-pattern transects by 90° between visits, as well as the time of the day of the visit, to maintain unpredictability. Due to man power limitations in 2014 we could only apply the treatment to 6 plots, while in 2015 the treatment was applied to all 12 plots. The six split-plots which were “disturbed” in 2014 became control split-plots the next year and vice versa. This experiment was approved by the local authorities and the French ringing scheme C.R.B.P.O. “Centre de Recherches sur la Biologie des Populations d’Oiseaux” (permit number 2014157-0012 of the “Direction Régionale de l’Environnement, de l’Aménagement et du Logement de Franche-Comté” and permit number 15006 for blue- and great tits (*Cyanistes caeruleus* and *Parus major*, respectively) for 2014-2016 from the C.R.B.P.O., for details see also Bötsch et al., 2017).

Blood sampling

From 20 April all 210 nest boxes were checked every second week. Nest boxes with full clutches were checked daily around the estimated hatching date to determine the exact hatching date. Blue- and great tit chicks were blood sampled at the age of six days (mean=6.2 days, sd=0.6), when they were large enough to bear blood-sampling but still have underdeveloped immune systems, thus still maintaining the matAb titres (Grindstaff 2008; Hasselquist & Nilsson 2009; King, Owen & Schwabl 2010). All chicks of a brood were weighed to the nearest 0.1g with a digital balance and a subsample of 1 - 5 chicks per brood were blood sampled through vein puncturing with a 0.3 mm syringe at the metatarsus and collecting the effluent blood with a heparinized capillary. Up to 40 µl were sampled and directly centrifuged in the field for 5 minutes at 8000 rpm (Hettich, EBA 3S) to separate the plasma from the cells. Both blood cells and plasma were then stored in liquid nitrogen or deep freezers (-20°C) until analysis.

When chicks were 15 days old, they were weighed again and ringed with an aluminium ring from the C.R.B.P.O. The number of ringed chicks per nest box served as

surrogate for the number of fledglings, since chick mortality at this stage is assumed to be low (Lindén, Gustafsson & Pärt 1992; Oddie 2000). In 2015 we additionally marked blood-sampled chicks with small-coloured elastic bands and therefore could identify them individually when ringing. Therefore the analysis of growth and weight gain is only based on the second study year (2015).

Maternal antibody measurement

MatAbs were measured in the lab using an Enzyme-linked Immunosorbent Assay (ELISA). Plates with ninety-six-wells were coated with an anti-chicken IgG (Sigma C-6409) diluted 1:180 in a 0.05M carbonate buffer (pH 9.6) and incubated overnight at 4°C. Afterwards the plates were washed three times with PBS (Phosphate-buffered saline)/Tween20 (3x 250 µl) and blocked (for at least one hour at room temperature) with 250 µl 1% BSA (Bovine serum albumin) diluted in 0.01M PBS/Tween20 (from now on referred as BSA-PBS/Tween20). After being washed again, the test plasma was added to the wells. The plasma samples (3 µl) of blue tits were diluted 1:100 and those of great tits 1:500. For each sample 100 µl were added (in duplicates) to the wells (Diluent: BSA-PBS/Tween20), two wells were filled with the BSA-PBS/Tween20 buffer, as blanks and two wells were filled with an 1:160,000 diluted chicken plasma as internal control (Diluent: BSA-PBS/Tween20). On the same plate we added in duplicates a standard dilution series of a chicken plasma-pool: pure buffer as negative control and seven dilutions from 1:10,000 up to 1:640,000 (Diluent: BSA-PBS/Tween20). All plasma-sample measures were then expressed relative to this standard in units per µl. The plates were incubated for three hours at room temperature and afterwards washed again three times with 250 µl PBS/Tween20. Then 100 µl of 1:3000 diluted (BSA-PBS/Tween20) peroxidase-conjugated rabbit anti-chicken-IgG (Sigma A9046) was added to each well, except the blanks where 100 µl BSA-PBS/Tween20-buffer was added instead. The plates were incubated over

night at 4°C and again washed three times with 250 µl PBS/Tween20. Then 100 µl of the substrate solution was added. This substrate solution consisted of 20 ml citrate buffer (pH 4), 80 µl of 1:40 diluted 30% hydrogen peroxide (diluted in distilled water) and 200 µl ABTS (2,2'-azino-bis(3-ethylbenzothiazoline-6-sulphonic acid)). The plate was then put for 15 min on a plate shaker and the absorbance measured with an ELISA plate reader at 405 nm (BIO-RAD, Benchmark Microplate Reader). For all the consecutive analyses the mean of the duplicate measures were computed.

Vegetation mapping

In June 2015 we conducted a vegetation survey. With a stratified random sampling we distributed one survey point per 0.5 ha (n=210) and measured the following habitat variables: ground cover (%) on a 2x2m area, shrub cover (%) on a 3x3m area, number of trees (diameter at breast height > 5 cm) per species and standing deadwood on a 8x8m area and canopy cover (% by looking straight up to the canopy and estimating the amount of covered sky by the canopy in the observer's visual field). The vegetation measures were averaged within each split-plot, and from these means we computed a Principal Component Analysis (PCA). Since the first axis of the PCA explained 59% percent of the variation by itself, we used only the first axis score for further analyses.

Statistical analyses

Only first broods with at least one egg laid during the experimental disturbance period were used (see Fig. 1). Predated broods were excluded from all analyses since they do not reflect the effect of human disturbance. All analyses were done using the lme4-package in R 3.3.0 (Bates *et al.* 2015; R Core Team 2016). To investigate the potential effect of the experimental disturbance on matAbs in great- and blue tit chicks, we used two linear mixed models (Table 1). MatAb measures were log (natural logarithm) transformed to fulfil model assumptions. As explanatory variables we included the two-

level factor *disturbance* (disturbed vs. control split-plots), the vegetation, as the first principal component of the vegetation PCA (*First principal component (vegetation)*) and the interaction between disturbance and vegetation. Furthermore we tested for the linear and quadratic effect of laying date of the first egg (*Julian date first egg*, *Julian date first egg*²), the distance to the nearest gravel road (*Distance to road [m]*), the *chick age* and the difference in body mass between the measured chick and its heaviest sibling (*Difference in body mass to heaviest sibling [g]*), as a surrogate for hatching order. To account for the stressful effects of competition, we included the number of occupied nest boxes (independent of the species) within a 100m radius (*total number of occupied neighbouring nest boxes*), as a nest-box specific measure of breeding density. Given that among tits, great tits appear to have the most dominant behaviour we also tested for the proportion of nest boxes per split-plot that were occupied by great tits (i.e. number of nest boxes occupied by great tits divided by all occupied nest boxes occupied in a split-plot; *relative GT occupancy*).

For the analyses investigating the relationship between matAbs and hatching success in both great and blue tits, we used two generalized linear mixed models with a binomial error distribution (Table 2), in which hatching success was introduced as number of hatchlings divided by the number of eggs (clutch size). Since not all broods were sampled for matAbs at the same exact age, the effect of matAbs was included in this model as the residuals of the linear model regressing average matAb titres per brood against average chick age per brood (with th); *Residuals of mean Ab titre*). We also controlled for the effect of *Relative GT occupancy*, *total number of occupied neighbouring nest boxes*, *Julian date first egg*, *Julian date first egg*², *Distance to road [m]* and *First principal component (vegetation)*.

In the four aforementioned models we accounted for the non-independence of the different years and nest boxes by including the random factors year and a random factor

nest-box-ID, nested within split-plot-ID, nested within plot-ID. To account for the non-independence of matAb measures between plates and runs (several plates per lab run), we included in the first two models a random factor plate-ID, nested within batch-ID. For the two models on hatching success, we accounted for this non-independence of plates with the same random factors already in the linear model where we computed the residuals (*Residuals of mean Ab titre*).

In order to examine the relationship between matAbs and chick growth we performed two different types of models (Table 3). First, we modelled the variations in chick growth with matAbs by including an interaction between the natural logarithm of chick age and the matAb titre (*MatAb titre [units μl^{-1}] \times log (Chick age)*). We also accounted for the effect of *Relative GT occupancy*, *Total number of occupied neighbouring nest boxes*, *Julian date first egg*, *Julian date first egg²*, *Distance to road[m]* and vegetation (*First principal component (vegetation)*). Moreover, we also tested for the effect of brood size on growth by including the number of fledged chicks (*Number of fledglings*), and the effect of time of the day on chick mass (*Minutes since sunrise*) both alone and in interaction with the natural logarithm of chick age (*Minutes since sunrise \times log (Chick age)*). To account for the non-independence of multiple chick measures, we included as random factors chick-ID nested within nest-box-ID, nested within split-plot-ID, nested within plot-ID. Since these data were available only in 2015, it was not necessary to introduce the year effect. Secondly, we did a similar model with the same explanatory variables, but with body mass gain per day as response variable. This variable was calculated as the difference in body mass between the two measures divided by the difference in chick age (days) and followed a normal distribution. Since in this case chick age was already offset in the response variable, the two interactions from the precedent model ceased. Consequently the matAb titre (*MatAb titre [units μl^{-1}]*) was now included as additive factor, whereas daytime (*Minutes since sunrise*) was not included anymore as we

computed the change in body mass over several days and the random factor chick-ID was not necessary anymore.

For allowing proper interpretation of the models, especially when including an interaction, we computed 95% credible intervals (CrI) and posterior-probabilities using a Bayesian framework. Therefore we simulated 10,000 random samples from the joint posterior distribution of the model parameters using the `sim`-function from the `arm`-package (Gelman & Su 2015) and computed the 95% CrI (lower and upper limit, 2.5% and 97.5% quantiles, respectively). For the posterior probabilities we computed the mean of the 10,000 differences between “disturbed” and “control” estimates, which were different from zero (either larger or smaller than zero). The resulting probability lies between 0.5 and 1 and is a measure for the strength of the difference, with larger values representing a stronger difference.

RESULTS

The experimental disturbance resulted in a reduction of matAbs in young nestlings, compared to control broods, in great tits, but not in blue tits (Fig. 2, Table 1). The interaction between disturbance and the first principal component (vegetation) for great tits showed that vegetation density (the *First principal component (vegetation)* is highly correlated with shrub-cover) modulated the impact of disturbance on matAb transmission (Fig. 3, Table 1). In the case of the blue tit, we did not find an effect of the experimental disturbance, but there seemed to be a negative effect of the relative density of breeding great tits on matAbs (Fig. 4, Table 1). For both species Julian date of the first egg had a positive effect on matAb titres while the difference to the heaviest sibling had a negative effect (Table 1). We also found a positive effect of chick age on the matAb titre for great tits (Table 1).

We found a positive correlation between matAb titres and hatching success for great tits, but not for blue tits (Fig. 5 and Table 2). For great tits, we also found that the proportion of nest boxes occupied by conspecifics and the total number of occupied nest boxes in the near surroundings both had a negative effect on hatching success (Table 2).

For both species we found that matAbs were positively correlated with chick body mass (Fig. 6 A,B and Table 3). At day six larger chicks had higher matAb titres, but these positive relationships disappeared towards fledging (Fig. 6 A,B) due to a lower variability in fledgling body mass. This translated in an overall lower body mass gain in chicks with higher matAb titres as shown in the negative correlation between body mass gain per day and matAb titres at day six (Fig. 6 C,D and Table 3). We also found a quadratic effect of Julian date of the first egg on body mass gain for both tit species, which implies that the earliest and latest broods show a higher weight gain per day as the broods in the middle of the season (Table 3).

DISCUSSION

In this study we showed that experimental human disturbance during egg-laying reduced antibody titres in great tit chicks. We hypothesize that human disturbance increased circulating corticosterone in laying females, reduced their antibody titres through the immunosuppressive action of corticosterone, and in turn reduced the amount of antibodies transferred to eggs. We could not confirm the exact mechanism since, to prevent nest abandonment and reduce additional sources of stress (i.e. beyond the experimental disturbance), we could not capture laying females to measure their corticosterone levels. However, corticosterone is known to be released in stressful situations, including disturbance by humans (Müllner, Linsenmair & Wikelski 2004; Almasi *et al.* 2015). The immunosuppressive effect of corticosterone has been shown by several authors (see for example Rubolini *et al.*, 2005; Saino *et al.*, 2003; Stier *et al.*, 2009). Thus, we think that this physiological cascade is a likely mechanism through which our experimental disturbance resulted in lower matAb titres in chicks. In line with others, we also found an effect of laying order on matAb titres, with later hatched chicks (assuming representing the laying order) having lower matAb titres (Hayward & Wingfield 2004; Love *et al.* 2008).

Moreover, we found that the effect of human disturbance was not homogeneous throughout space, but that it depended on the type of vegetation. We found that higher amounts of shrub vegetation lowered the negative impact of the disturbance on matAb titres. Vegetation may have acted as protective shield, buffering the stress caused by human presence (Tablado & Jenni 2017). Interestingly, we did not find the same pattern in blue tits. In this case we did not find an effect of the disturbance treatment or interaction with vegetation on matAbs in nestlings, but we found an effect of the relative abundance of great tits in the split-plot. A plausible explanation for this would be that great tits are an important biological stressor for blue tits, and thus, the presence of great tits is overriding

or obscuring the negative effects of human presence. Great tits are dominant over blue tits. Our nest boxes had an entrance diameter which permitted both species to enter the nest box and great tits have been shown to suppress the settlement of blue tits (Löhrl 1977).

We also found a positive correlation between matAb titres and the hatching success for great tits. This could be due to several reasons. MatAbs might protect from infections, which would otherwise cause the death either of the embryo or the freshly hatched young. Note that we counted the number of hatchlings at day six, and therefore we do not know whether failed eggs or dead young chicks caused the difference between clutch size and number of “hatchlings”. Additionally matAbs could be correlated with other non-measured variables. That is, chicks with lower matAb titres could be linked to more stressed mothers which are likely to have laid lower quality eggs and/or transmitted more corticosterone into eggs, thus resulting in lower hatching success (Hayward & Wingfield 2004).

Similarly, we found a positive correlation of matAbs and body mass at day six, which was lost at later ages, which translated into reduced body mass gain with time in larger freshly hatched chicks. This coincides with the findings of Ismail et al., (2015). They suggested a cost of maternal antibodies on body mass gain. However, in our case it seems to be due to chicks with larger amounts of matAbs being also the largest chicks and thus to gain less mass to reach fledging body mass than smaller chicks (see Fig 6. C,D).

Whether human recreation trans-generationally negatively affects birds, through changes in matAb deposition clearly also depends on several modulators. These include the disturbance intensity, the type of human recreation activity, the mother's stress tolerance, e.g. habituation towards humans and, as we could show, the vegetation density, as denser vegetation lowers the disturbance impact. There are also other factors than disturbance, driving matAb titres, like body condition of the mother (e.g. food availability),

clutch size or the health status of the mother in general (Klasing & Leshchinsky 1998; Grindstaff, Brodie & Ketterson 2003; Boulinier & Staszewski 2008; Hasselquist & Nilsson 2009).

Up to now effects of human disturbance on reproduction mainly occurred through prevention of feeding, interruption of incubation or indirectly via noise (Safina & Burger 1983; Zanette *et al.* 2011; Schroeder *et al.* 2012). In this study, we could show that human disturbance affects matAb titres and that these affect hatching rate, body mass gain and therefore probably also survival (see Pihlaja *et al.*, 2006). If the disturbance would continue through the entire breeding season, potentially the catch up in body mass, as we found, would not be possible. Therefore we propose that this cascade of stress, via corticosterone, and reduced matAb titres, depicts a new way of how human disturbance affects reproduction.

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TABLES

Table 1: Model estimates with their corresponding 95% credible intervals (CrI) of the matAb model examining the effect of experimental disturbance.

The reference categories are nests from control split-plots. The factor level of each categorical variable is given in parenthesis. GT: Great tit, BT: Blue tit.

Variable	GT estimate	GT 95% CrI	BT estimate	BT 95% CrI
Intercept	5.402	5.120; 5.674	4.030	3.659; 4.413
First principal component (vegetation)	-0.007	-0.139; 0.121	-0.076	-0.300; 0.143
Disturbance (disturbed)	-0.127	-0.279; 0.025	0.053	-0.201; 0.308
Julian date first egg	0.212	0.099; 0.328	0.178	0.006; 0.346
Julian date first egg ²	-0.054	-0.123; 0.015	-0.042	-0.182; 0.102
Distance to road [m]	-0.010	-0.099; 0.078	0.052	-0.080; 0.184
Difference in weight to heaviest sibling [g]	-0.223	-0.265; -0.179	-0.106	-0.175; -0.035
Chick age	0.130	0.020; 0.244	0.118	-0.087; 0.320
Relative GT occupancy	-0.045	-0.157; 0.072	-0.224	-0.478; 0.022
Total number of occupied neighbouring nest boxes	-0.003	-0.087; 0.080	0.058	-0.080; 0.189
First principal component (vegetation) × Disturbance (disturbed)	0.243	0.068; 0.421	0.089	-0.149; 0.328

Distribution: normal; random factors: year and nest box ID nested within split-plot ID nested within plot ID and plate ID nested within batch ID.

Table 2: Model estimates with their corresponding 95% credible intervals (CrI) for the analysis of hatching success depending on matAbs. GT: Great tit, BT: Blue tit.

Variable	GT estimate	GT 95% CrI	BT estimate	BT 95% CrI
Intercept	2.651	2.302; 2.998	2.050	1.636; 2.471
First principal component (vegetation)	-0.049	-0.327; 0.234	-0.054	-0.375; 0.267
Residuals of mean Ab titre	0.223	-0.018; 0.462	-0.172	-0.507; 0.170
Relative GT occupancy	-0.348	-0.665; -0.033	-0.172	-0.589; 0.243
Total number of neighbouring occupied nest boxes	-0.243	-0.471; -0.005	0.158	-0.204; 0.521
Julian date first egg	-0.045	-0.345; 0.262	0.063	-0.278; 0.412
Julian date first egg ²	-0.018	-0.225; 0.189	-0.088	-0.375; 0.193
Distance to road [m]	0.177	-0.074; 0.427	0.050	-0.289; 0.379

Distribution: binomial, link function logit; random factors: year and nest box ID nested within split-plot ID nested within plot ID.

Table 3: Estimates of the body mass development and body mass gain models depending on matAb titres with their corresponding 95% credible intervals (CrI) for great tits (GT) and blue tits (BT).

Variable	GT estimate	GT 95% CrI	BT estimate	BT 95% CrI
Effect on body mass development ^a				
Intercept	-12.429	-13.505; -11.322	-6.275	-8.219; -4.365
First principal component (vegetation)	-0.078	-0.239; 0.080	0.011	-0.331; 0.352
MatAb titre [units μl^{-1}]	0.020	0.016; 0.024	0.053	0.027; 0.079
Log (Chick age)	11.603	11.127; 12.070	7.013	6.212; 7.838
Minutes since sunrise	-0.104	-0.643; 0.426	0.178	-0.625; 0.966
Relative GT occupancy	0.095	-0.057; 0.246	0.115	-0.214; 0.448
Total number of occupied neighbouring nest boxes	0.067	-0.089; 0.222	-0.087	-0.401; 0.227
Julian date first egg	0.150	-0.008; 0.302	-0.026	-0.324; 0.265
Julian date first egg ²	-0.036	-0.167; 0.097	-0.386	-0.698; -0.082
Number of fledglings	0.017	-0.135; 0.170	-0.089	-0.384; 0.211
Distance to road [m]	-0.049	-0.200; 0.105	-0.058	-0.375; 0.254
MatAb titre [units μl^{-1}] \times log (Chick age)	-0.007	-0.009; -0.006	-0.021	-0.032; -0.010
Minutes since sunrise \times log (Chick age)	0.153	-0.076; 0.387	-0.147	-0.483; 0.199
Effect on body mass gain per day ^b				
Intercept	1.213	1.148; 1.277	0.733	0.616; 0.854
First principal component (vegetation)	-0.010	-0.043; 0.022	-0.020	-0.074; 0.033
MatAb titre [units μl^{-1}]	-0.001	-0.001; -0.001	-0.003	-0.005; -0.002
Relative GT occupancy	-0.001	-0.031; 0.028	-0.011	-0.063; 0.043
Total number of occupied neighbouring nest boxes	-0.022	-0.051; 0.007	-0.005	-0.066; 0.056
Julian date first egg	-0.009	-0.038; 0.021	0.042	-0.017; 0.099
Julian date first egg ²	0.026	0.002; 0.050	0.079	0.020; 0.139
Number of fledglings	-0.012	-0.040; 0.017	0.028	-0.032; 0.088
Distance to road [m]	0.013	-0.017; 0.041	0.034	-0.023; 0.092

^a Distribution: normal; random factors: chick ID nested within nest box ID nested within split-plot ID nested within plot ID.

^b Distribution: normal; random factors: nest box ID nested within split-plot ID nested within plot ID.

FIGURES

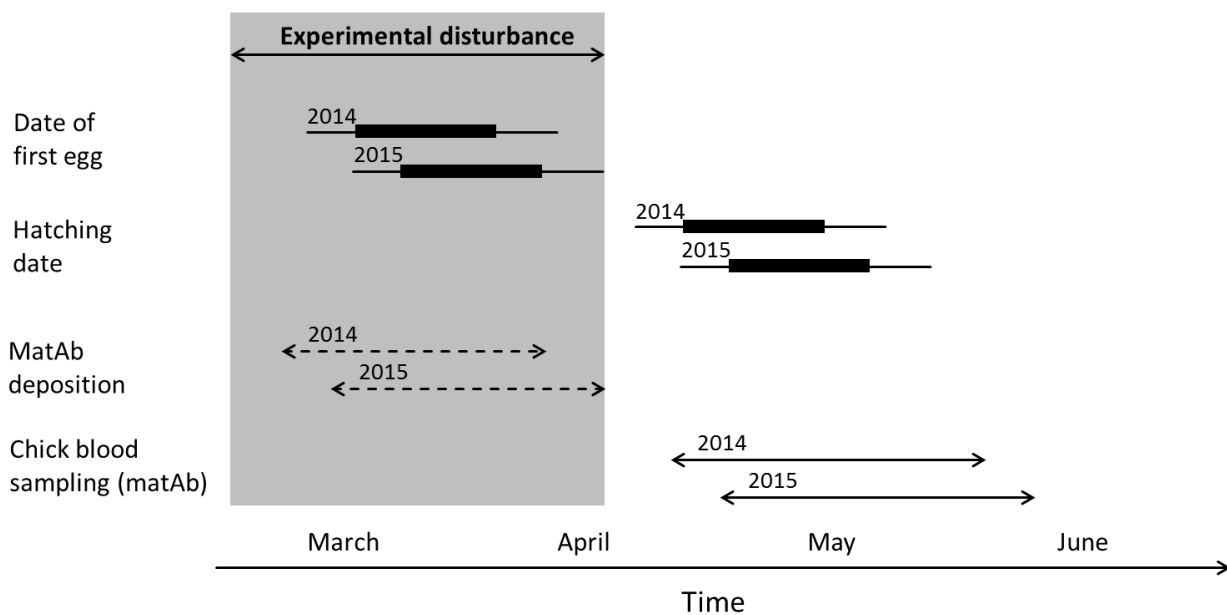


Fig. 1. Diagram of the temporal overlap of experimental disturbance (grey square) and breeding stages (egg-laying and hatching). Note that the deposition of the maternal antibodies (matAb) in eggs overlaps with the disturbance phase, whereas hatching and the following feeding period do not. Breeding in the second study year (2015) was about 1 week later than in the first study year (2014).

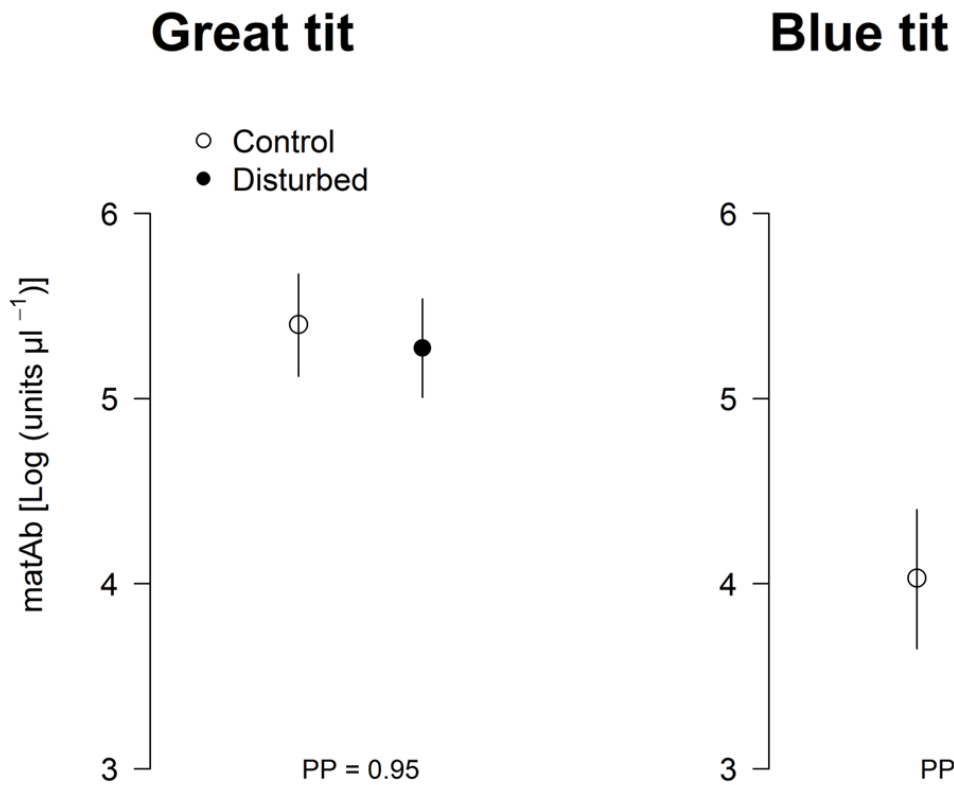


Fig. 2. Effect of experimental disturbance on matAb titres in tit chicks. Model estimates \pm 95% CrI of the species-specific matAb titres between disturbed and control split-plots with their corresponding posterior probability (PP). PPs can take values from 0.5 to 1 and the higher the probability, the stronger is the difference between treatments.

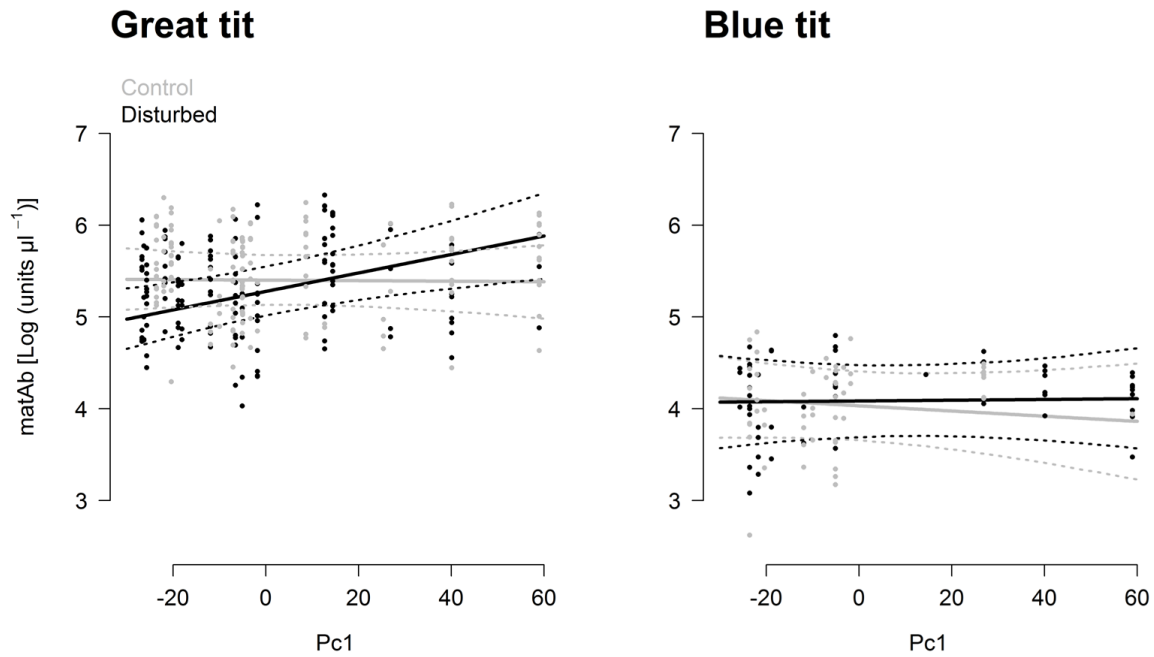


Fig. 3. Effect of experimental disturbance on matAb titres in tit chicks in relation to vegetation (Pc1). Model estimates (solid lines) \pm 95% CrI (dotted lines) of the species-specific matAb titres depending on Pc1 between disturbed and control split-plots. Pc1 is positively correlated with shrub cover and negatively with ground cover and canopy cover, therefore representing a measure for visibility. The dots represent the data points (grey: control split-plots, black: disturbed split-plots).

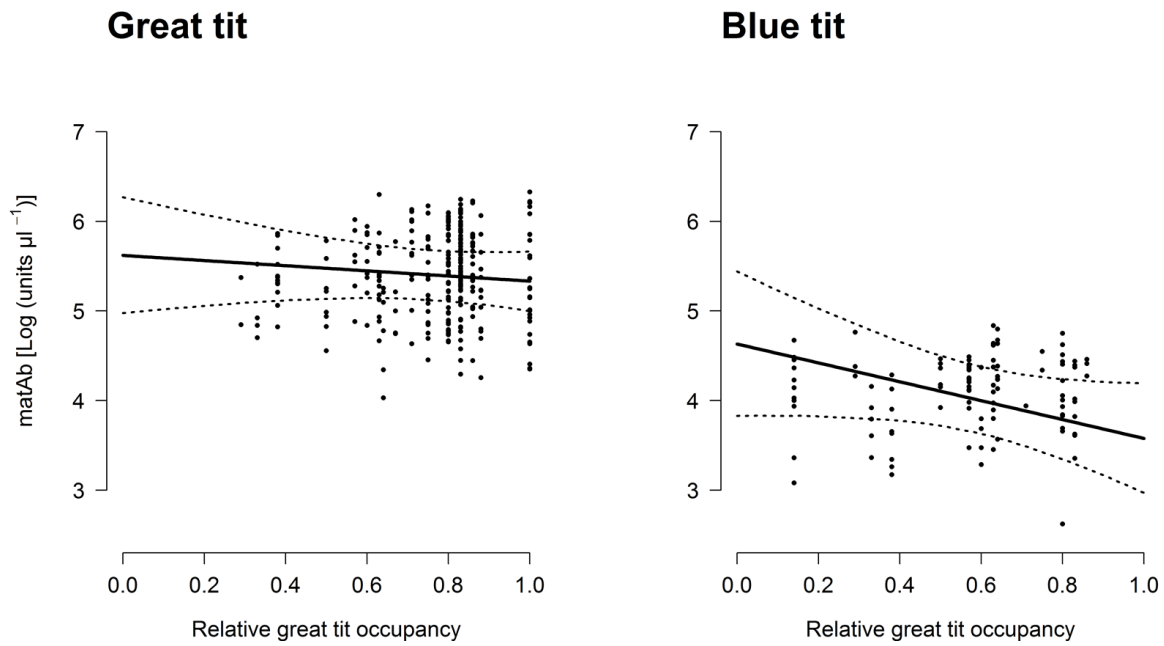


Fig. 4. Effect of the split-plot specific relative great tit nest box occupancy on species-specific matAb titres in chicks. Represented are model estimates (solid lines) \pm 95% CrI (dotted lines). The dots represent the data points.

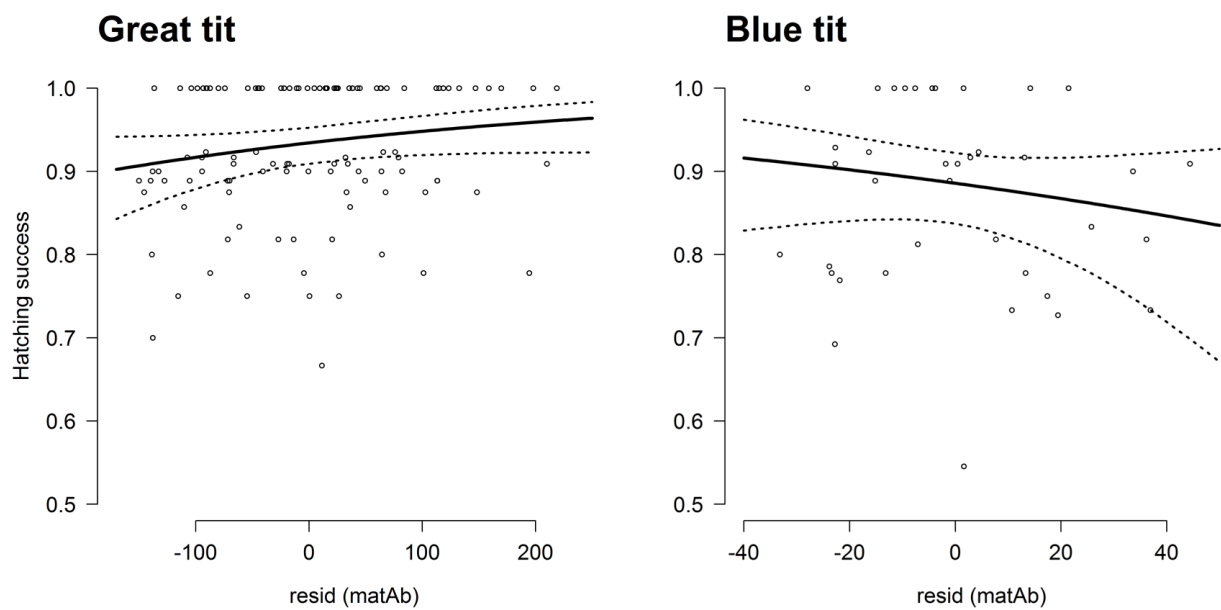


Fig. 5. Effect of matAb titres on hatching success. Model estimates for hatching success (with corresponding 95% CIs; dotted lines) depending on mean matAb titres per brood (solid lines). Plotted are the matAb residuals (resid (matAb)) corrected for chick age. Open circles depict the data points. Note the different x-axes ranges.

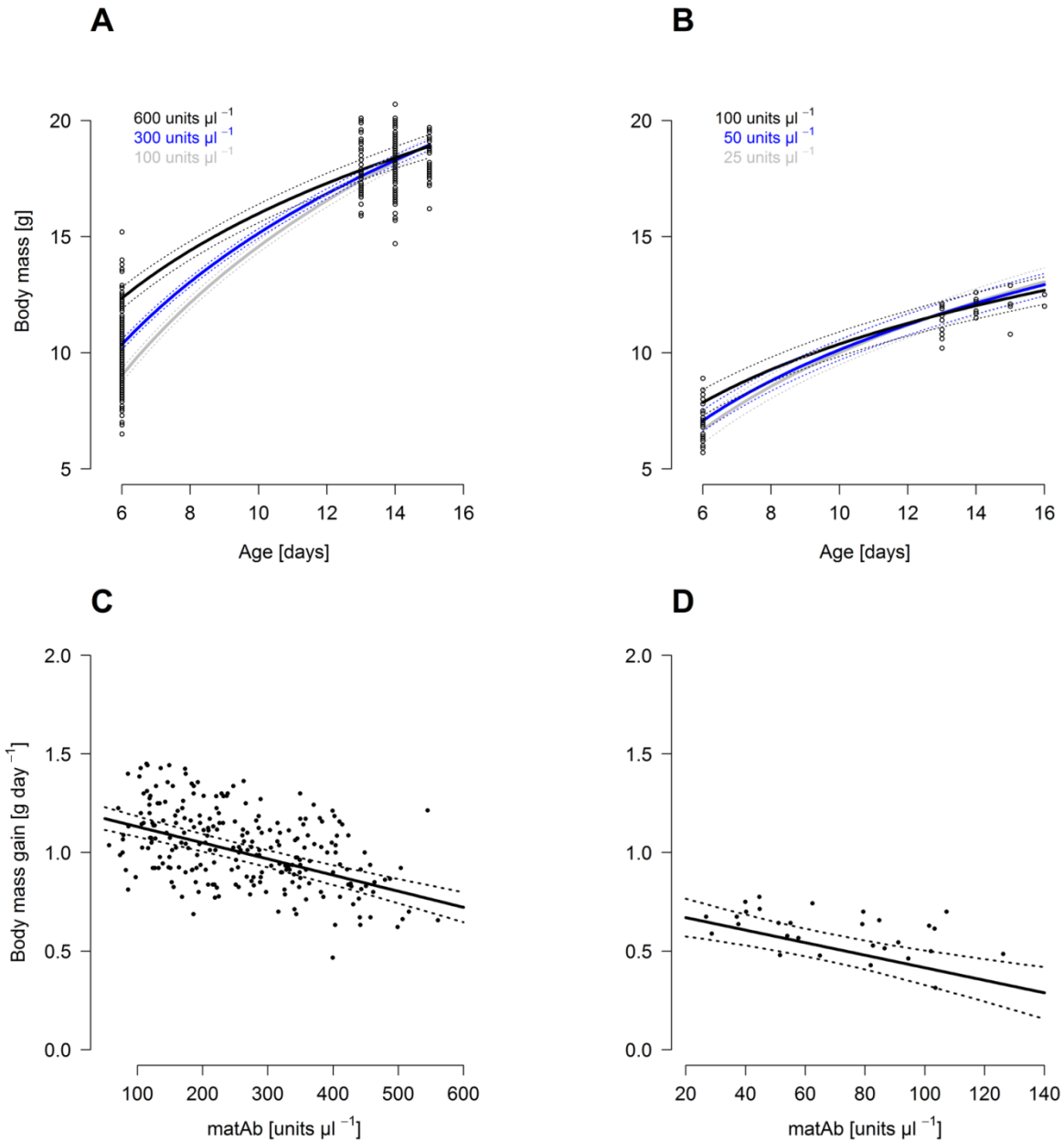


Fig. 6. Body mass development and daily body mass gain until fledging, dependent on matAb titres. A and B: Model estimates \pm 95% CrI of chick body mass development from day six until fledging, depending on matAb titres (three selected species-specific titres shown). C and D: Model estimates \pm 95% CrI of chick body mass gain per day depending on matAb titres. A and C: Great tits (*Parus major*), B and D: Blue tits (*Cyanistes caeruleus*), open/closed circles represent the data points. Note the different x-axis ranges for figures C and D.

GENERAL DISCUSSION

Diverse outdoor recreational activities are widely practiced, have many followers and affect most habitats during many (sometimes all) periods of a year. Wildlife is therefore confronted with humans almost continuously and, even when not suffering from consumption (e.g. hunting, fishing), face direct effects through human encounters or get indirectly affected through changes in their habitat (Wilkes 1977; Boyle & Samson 1985; Reed & Merenlender 2008). However, these effects are not always obvious or well-known. Although a lot of research has been done to investigate these effects, studies so far, have neglected two aspects: 1) disentangling the effects of direct human presence from those of habitat modifications linked to recreation and 2) considering the effects of low levels of disturbance, as most studies focus on areas with an already considerable amount of disturbance. In this thesis we tackled these problems by using a combination of well-thought comparative studies and experiments in the field.

Disentangling direct from indirect disturbance effects

We define an indirect human impact as an impact of humans on a resource (e.g. habitat (vegetation), food, nesting sites, or flows of communication) of a given species which, via changing these resources, affects the individual. One of the most common indirect impacts of human recreation is the construction of trails. Firstly, trails entail a habitat change by clearing the vegetation or just by repeated trampling by humans (Monz, Pickering & Hadwen 2013). Secondly, previously connected habitat gets split into fragments, which may reduce animal movements and therefore population connectivity, which results in reduced gene flow (Saunders, Hobbs & Margules 1991; Reed, Johnson-Barnard & Baker 1996; Forman & Alexander 1998; Bregman, Sekercioglu & Tobias 2014). The severity of trail impacts clearly depends on their extent (e.g. width, coating) and also on the species characteristics (small versus large and highly mobile versus less mobile).

Thirdly, depending on the habitat, clearing of the natural vegetation results in changes in abiotic factors, such as light conditions, water balance or temperature (Trombulak & Frissell 2000). These changes in conditions promote a change in vegetation along trails, with potentially negative or positive effects on birds.

By comparing areas with similar types of trails but differences in human frequentation, we were able to separate the effect of the trail *per se* from the effect of the presence of people. Our study comparing bird compositions between forests with different intensities of human use showed that most birds avoided sites close to trails when they were heavily used by humans, but not when human passages were very infrequent. This finding implies that in these forests, although used for recreation since many years, humans still scare off many birds and that they apparently did not entirely habituate to these activities.

On the other hand the changes in vegetation through trails, leads to trail-proximate habitats becoming more suitable for some species (e.g. ground nesters) but less for others. Ground nesters may profit from trail edges, as the improved light conditions favour ground vegetation, compared to the dark interior of forests, which promotes better nesting sites. We found that in our study ground nesters indeed preferred areas close to trails, however only for trails with low frequentation. Still, the most apparent finding was, apart from changes in vegetation through trails, that the humans using these trails are the much stronger factor driving bird communities. The important effect of the degree of human frequentation on trails could also explain why different studies looking at trail impacts found opposing results (Miller, Knight & Miller 1998; Deluca & King 2014). Although trails might have substantial effects through changes in vegetation, and through promoting access into forests for both humans and certain predators, they also guide recreationists through space and since most of them stay on the trails, they reduce the negative effects

of human off-trail activities (Coppes & Braunisch 2013). This also facilitates wildlife habituation as the human movements on trails become predictable (Taylor & Knight 2003).

Effects of human recreation in previously undisturbed areas

By comparing the antipredator response of birds in areas with and without recreation, we were able to confirm that the impact of human disturbance might be obscured in areas where recreation has been already established for a long time. Our study showed that in areas with a high human frequentation, species tolerated a closer human approach before fleeing than in areas largely unfrequented by humans. This could be explained by two different processes. First, behavioural habituation towards human presence can occur, where birds learn that humans are not dangerous and reduce their reactions. This has been shown to strongly depend on the species as well as on individual personality (Walker, Dee Boersma & Wingfield 2006; Rodríguez-Prieto, Martín & Fernández-Juricic 2011; Samia *et al.* 2015; Vincze *et al.* 2016). Secondly, it may occur through selection of certain individuals that are more human tolerant (Carrete & Tella 2013; Miranda *et al.* 2013; Sprau & Dingemanse 2017). This entails directional selection towards human tolerant individuals in human frequented habitats, which would drive evolution and therefore reduce the diversity of personalities (like Allendorf and Hard, 2009 showed for harvested animals). These variations of reactions in birds depending on human frequentation would partially explain why some studies found effects on birds at certain levels of human recreation while other did not.

Therefore, in order to study the real magnitude of the effect of human disturbance, we chose the forest that had very low numbers of visitors to experimentally test the effect of low levels of disturbance. With our experimental study we showed that human recreational activities (hiking in our study), negatively affected forest bird territory establishment. Consequently reduced breeding bird densities and species richness were

the outcomes. The season during which a disturbance event happens and its intensity clearly have an important influence on the strength of its impact (Tablado & Jenni 2017). Apparently the pre-breeding period is very important for birds, as they then decide where to breed and this finally can affect their fitness. These findings can only be the result of a direct human disturbance effect, as there was no change in habitat resulting from our hikes.

Our disturbance intensity was quite low (two to three passages per day) and not representative for recreational hotspot areas. Still, we found that even low disturbance intensities can have severe impacts on bird territory establishment. In theory different relationships between disturbance intensity and impact severity have been proposed (Figure 1, adapted after: Monz et al., 2013; Steidl and Powell, 2006; Steven et al., 2011).

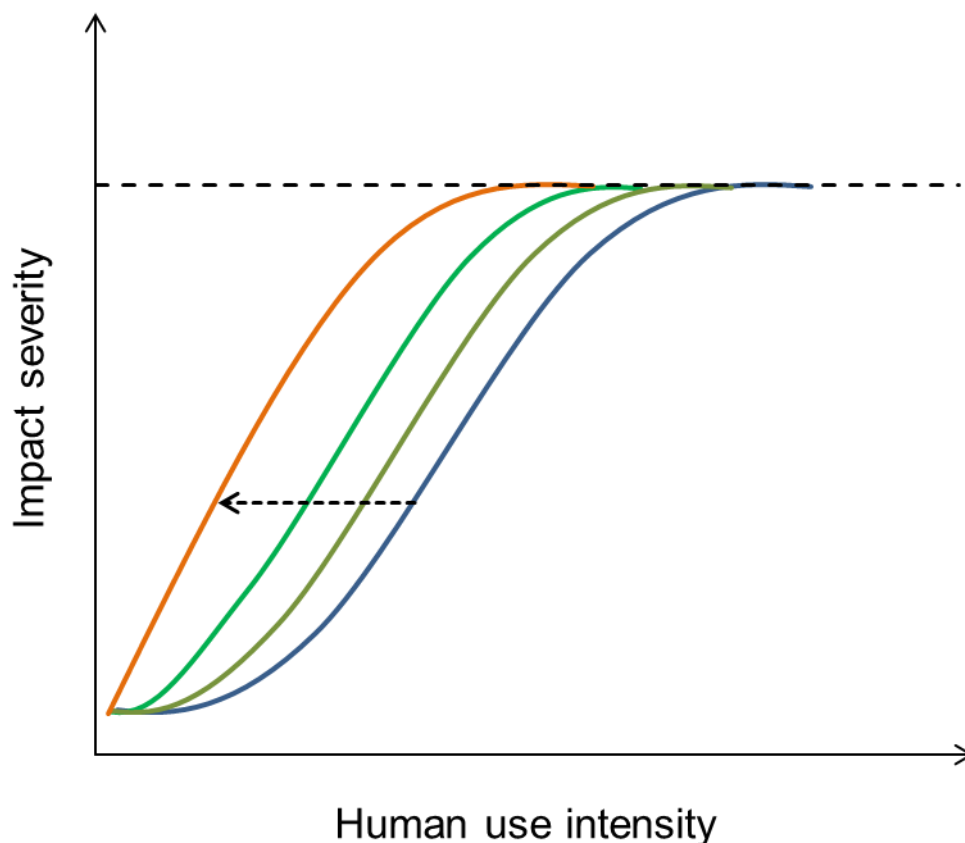


Figure 1: Generalizations of the impact of human disturbance on the severity of its impact. The dotted arrow indicates the direction from more to less experience with humans. The dotted line depicts a theoretical impact maximum.

The impact severity at low disturbance levels therefore depends on the shape of the curve (Figure 1) which likely depends on the species, the season (pre-breeding in our case), and also on the individuals former experience with human recreation. What actually drives the shape of this curve is an open question, which needs further investigation, especially concerning wildlife.

With our experiments we also could show that even low levels of disturbance can lead to trans-generational effects through variations in maternal antibody deposition into eggs by disturbed females. Mechanistically this could be driven via corticosterone, the main glucocorticoid in birds, which has an immunosuppressive function. That is, human presence would stress birds, leading to an increase in the release of corticosterone (Thiel *et al.* 2008; French *et al.* 2010; Almasi *et al.* 2015; Arlettaz *et al.* 2015). This increased corticosterone level in turn, would work as an immuno-suppressive agent reducing the antibodies available to be deposited into eggs (maternal antibodies; French *et al.*, 2010; Pihlaja *et al.*, 2006; Saino *et al.*, 2003). The species or site specific short-term reactions (physiological and/or behavioural) can be unimportant for an individual's survival, but not for its offspring where even short changes in parent behaviour can have drastic impacts (Zanette *et al.* 2011).

Conclusions and implications for conservation

Human outdoor recreation often has a negative impact on birds and it is likely to continue increasing in the future. In order to mitigate human recreation impact on wildlife, conservation measures have to be implemented specifically adapted to the season, the recreational activity type and the target species. In general, visitor guidance along or through rare habitats is highly recommended to keep the negative impacts through human recreation as low as possible. Human disturbances can already have severe impacts at

low intensities and short duration; therefore also research(er) related impacts have to be taken into account (Götmark 1992; Giese 1996).

Restricted access or at least stay-on-trail directives are valuable and often necessary conservation measures. Therefore also trail networks should not be too dense and if new trails have to be constructed the surrounding habitats and the local species' requirements should be taken into account (Rodríguez-Prieto *et al.* 2014). Also timber harvesting roads should be re-built/renaturalized to firstly limit the direct impact on the habitat and secondly to not promote human and predator access into before undisturbed areas. Trail effects should also be taken into account for bird monitoring schemes which are often conducted from trails or roads, where local abundance and species richness can be affected too (Hanowski & Niemi 1995; Šálek, Svobodová & Zasadil 2010).

Human presence can have short time effects like physiological or behavioural reactions, which might not severely affect the individual directly, but which might affect the offspring (trans generational effect, as we could show with maternal antibodies) or the individuals fitness via reduced breeding success (Pihlaja, Siitari & Alatalo 2006; French *et al.* 2010; Almasi *et al.* 2015). Such impacts are much harder to detect and to investigate and might only gradually impact populations (Blickley *et al.* 2012). Permanent, high intensity recreational activities, on the other hand, can trigger physiological reactions which lower apparent survival, force wildlife to adapt their behaviour (spatially and temporarily) or even cause animals to leave a given area (local extinction).

From time to time new outdoor activities pop up and sometimes get large numbers of followers like for example the recent trend for stand-up paddling (SUP). Such new activities might affect other habitat types or access new areas and therefore need to attract a conservationist's attention, which then should assess its impact. Conservation biologists should then propose conservation measures and support their implementation to "bridge the gap" between researchers and practitioners (Arlettaz *et al.* 2010).

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